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The Protocephalon: A Critique of Recent Interpretations[1]

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Introduction

The term "protocephalon" as used by Snodgrass (1938) applies to that portion of the head which lies anterior to the mandibular segment. As defined by him it is composed of the "prostomial acron" and a postantennal segment. The term "acron" has been used in somewhat different senses by different authors and to avoid confusion I have introduced the term "blastocephalon" instead. The *blastocephalon* may be defined as that portion of the head which includes the labrum, clypeus and occulo-antennal region. In the germ band it appears as an expanded anterior region, the cephalic lobes, which forms a sort of early embryonic head, hence the name. The posterior trunk-like region of the germ band may then be called the *blastocorm.*

The metameric composition of the protocephalon has long been a subject of controversy. Many embryologists claim to be able to distinguish a postantennal segment, and its presence in the embryo is almost universally accepted. The presence of a pair of coelomic sacs associated with the antennae was responsible for the theory that an antennal metamere, homologous with the first postoral metamere of the Annelida, enters into the composition of the head, but with increasing evidence that the antennae are the homologues of prostomial sense organs and not of segmental appendages some morphologists came to the conclusion that the entire blastocephalon is derived from the annelid prostomium which, with the first postoral segment (the postantennal), constitutes the protocephalon.

This view, however, is not generally accepted. Embryologists, who regard the presence of coelomic sacs or mesodermal somites as evidence of the inclusion of postoral segments in the head, propose other theories. Wiesmann (1926) described evanescent labral and preantennal sacs in addition to the antennal and postantennal, and other workers have described labral sacs in three other insects. These sacs have been interpreted as evidence of the presence of metameres in front of the antennal region. This poses a difficult problem: if the eyes and antennae are derived from prostomial organs, the occulo-antennal region must be derived from the prostomium, how then can there be metameres anterior to it?

Ferris (1946 *in litt.*) met this problem by proposing a new and revolutionary theory of polychaete segmentation and one of his students, Laura Henry (1947, 1948), in a comparative study of the nervous system of the annulates, claims to have obtained confirmation of this theory.

The first part of this paper will be concerned chiefly with a critical analysis of Henry's work. The second part will be concerned with recent differences of opinion on the morphology of the frons and clypeus in the definitive head.

The Segmentation of the Protocephalon

A. Constancy of Innervation

Henry's conclusions are based on the principle of the "constancy of innervation". This principle has long been used by vertebrate morphologists to establish the segmental homologies of muscles which, in spite of considerable

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shifts in position, are innervated by the nerve supplying the segment to which they primitively belong. Generally speaking, the ventral roots of the segmental nerves in vertebrates innervate only the muscle fibres of the corresponding somites. There are, however, important exceptions to this rule. The dorsal roots innervate a region of the skin corresponding to the somite, but there is some overlapping of adjacent nerves. It has been claimed that in insects also tegumentary nerves are not necessarily restricted to the segments to which they primitively belong. Ferris and Henry dispute this, but there is considerable evidence that the terminations of such nerves may extend into adjacent segments. A case in point is the innervation of the prothoracic glands in lepidopterous larvae. These are said to originate from the ectoderm of the labial segment, but they receive nerves from the suboesophageal, prothoracic and mesothoracic ganglia (Lee, 1948).

It is probable, however, that with some exceptions the nerves of segmental muscles are restricted to the neuromere of the segment to which the muscles belong and Ferris (1947) is therefore correct in stating that in the nervous system of the annulates we have "one of the most remarkable examples of stability and persistence of structure that are found anywhere in the animal kingdom." There can be little doubt that in the annulates, as in the vertebrates, there has been a constancy of innervation through a long evolutionary line, and Ferris and Henry have done good service to insect morphology by introducing this principle. Before accepting their conclusions, however, it is necessary to consider critically the conflicting evidence derived from other sources.

B. The Annelid Proboscis and Prostomium

Ferris and Henry's most revolutionary conclusion is that the proboscis of the Polychaeta (fig. 1B) is not an eversible portion of the stomodaeum but an invaginable portion of the body, and is composed of three segments. The first segment is reduced and represented only by the jaws; the second and third segments are well-developed and the "prostomium" is a dorsal lobe of the third. The third segment, except for the prostomium or head lobe, is retracted when the proboscis is invaginated and the apparent mouth lies ventral to the head lobe, its relation to this being similar to that of the mouth to the prostomium in the Oligochaeta. The prostomium in the latter group, however, is the first segment and, therefore, is not homologous with the head lobe of the Polychaeta.

A study of Henry's figures shows that she has strong evidence for this conclusion since each of the presumed segments of the proboscis is innervated

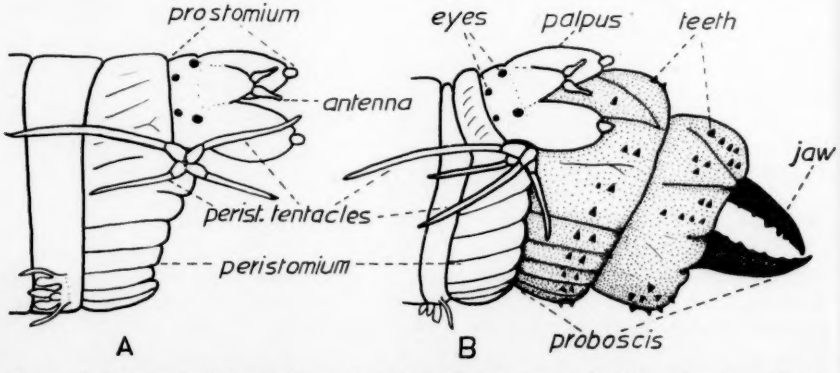

Fig. 1. Anterior end of *Nereis virens*. A with proboscis retracted, B with proboscis evaginated.

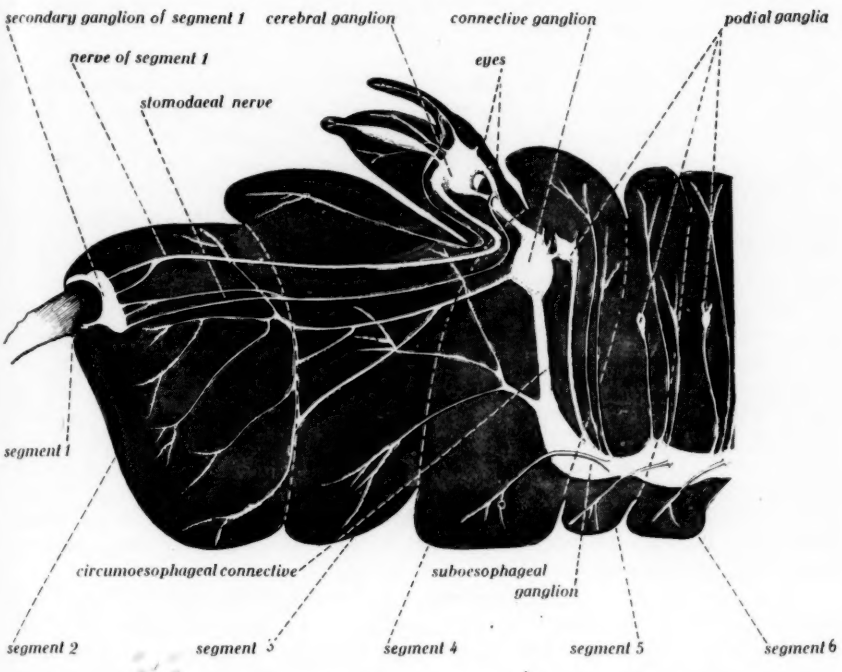

Fig. 2. *Nereis virens*, cephalic nervous system, lateral aspect (from Henry).

from a separate and distinct ganglionic mass (fig. 2). The stomodaeal nervous system is associated with the nerves of the first segment, an association used by Henry in identifying the first segmental ganglion throughout the arthropod group.

Granted the validity of the basic assumption, the constancy of innervation, the inferences drawn from the evidence appear to be legitimate, but these differ so markedly from the current concept of the morphology of the proboscis that they cannot be accepted or rejected finally until the evidence on which the current concept is based is re-examined critically and either refuted or confirmed.

Henry's interpretation of the segmentation of the insect protocephalon is based on her theory of the morphology of the polychaete proboscis. I shall attempt to show that even if this theory is accepted provisionally her conclusions on the segmentation of the insect head are not necessarily the only inferences that can be drawn from her evidence.

C. Theories of the Labrum and Clypeus

1. *Two independent segments*

Ferris (1942, 1943) is one of the chief exponents of the theory that the labrum and clypeus represent the first and second segments of the head. He believes that the principal transverse sutures of the head are intersegmental lines and therefore the clypeolabral and frontoclypeal sutures divide the anterior portion of the head into labral, clypeal and occulo-antennal segments. This conclusion was reached from comparative studies of the structure of the head

in insects and symphilids. Henry from her studies of the nervous system has reached the same conclusions.

The evidence on which Ferris and Henry base this theory is four-fold: (a) the presence of sutures which separate the labral, clypeal and occulo-antennal regions; (b) the discovery in the embryo of a few insects of one or two pairs of coelomic sacs anterior to the antennal sacs; (c) the presence in insects of the hypopharyngeal nerve, the apparent homologue of which in the Crustacea and Chilopoda innervates the clypeus also; (d) the innervation of the labrum by the nerve of the tritocerebrum which these authors believe to be the ganglion of the first segment.

(a) *Significance of the cranial sutures*

In considering the validity of the evidence from the sutures, it is necessary to remember that, in the annulates, mesodermal segmentation is normally accompanied by ectodermal segmentation which is manifested externally by intersegmental grooves and internally by the division of the nerve cord into neuromeres, each of which develops into the ganglion or nerve centre of the segment to which it belongs. It is also necessary to remember the phenomenon of recapitulation. A character which appears in the embryo of a primitive group of animals and persists to the adult stage may appear in a comparable stage of the embryo in a related higher group although it is absent in the adult. A character which goes far back in the ancestral line, if it appears at all, appears early in embryological development.

The blastocephalon of insects is externally unsegmented at a stage when the entire blastocorm, including the gnathocephalon, is distinctly segmented and superficially resembles the trunk region of the annelid. This suggests either that the blastocephalon is a single segment or that the external segmentation has been lost so completely and for so long a time that there is not even an evanescent segmentation in the early embryo. If such a primitive character as external segmentation is lost in the early embryo, its reappearance in the late embryo is extremely unlikely. We must hesitate therefore to accept the claim that the clypeolabral and frontoclypeal sutures are intersegmental grooves. It seems more probable that they are the result of secondary desclerotization or of inflection in a primitively continuous sclerite.

(b) *Labral and preantennal coelomic sacs*

There is as yet no evidence that mesodermal sacs anterior to the antennal sacs are generally present in the insect embryo. Where they occur there may be at least three possible explanations. (i) They may be the somites of persistent postoral metameres which have lost their external segmentation. This in effect is the interpretation accepted by Ferris, Henry and those embryologists who have described the sacs. (ii) They may be, as Snodgrass (1938) claims, portions of the blastocormic mesoderm which have extended forward into the blastocephalon and have become secondarily excavated. This theory apparently gains some support from the statement by Tiegs (1938) that in the embryo of *Calandra oryzae* the preoral mesoderm has a postoral origin. He claims that while the cells of the inner layer (mesoderm) spread over the ectoderm a small clump remains heaped up behind the developing stomodaeum. Later, cells from this clump spread forward around the stomodaeum and form two lateral sheets along the floor of the procephalic lobes (blastocephalon). These become united by transverse bands in front of the mouth. (iii) If we accept Henry's theory of the morphology of the polychaete proboscis and prostomium the so-called labral and pre-antennal sacs could be evanescent structures, a recapitulation of ancestral

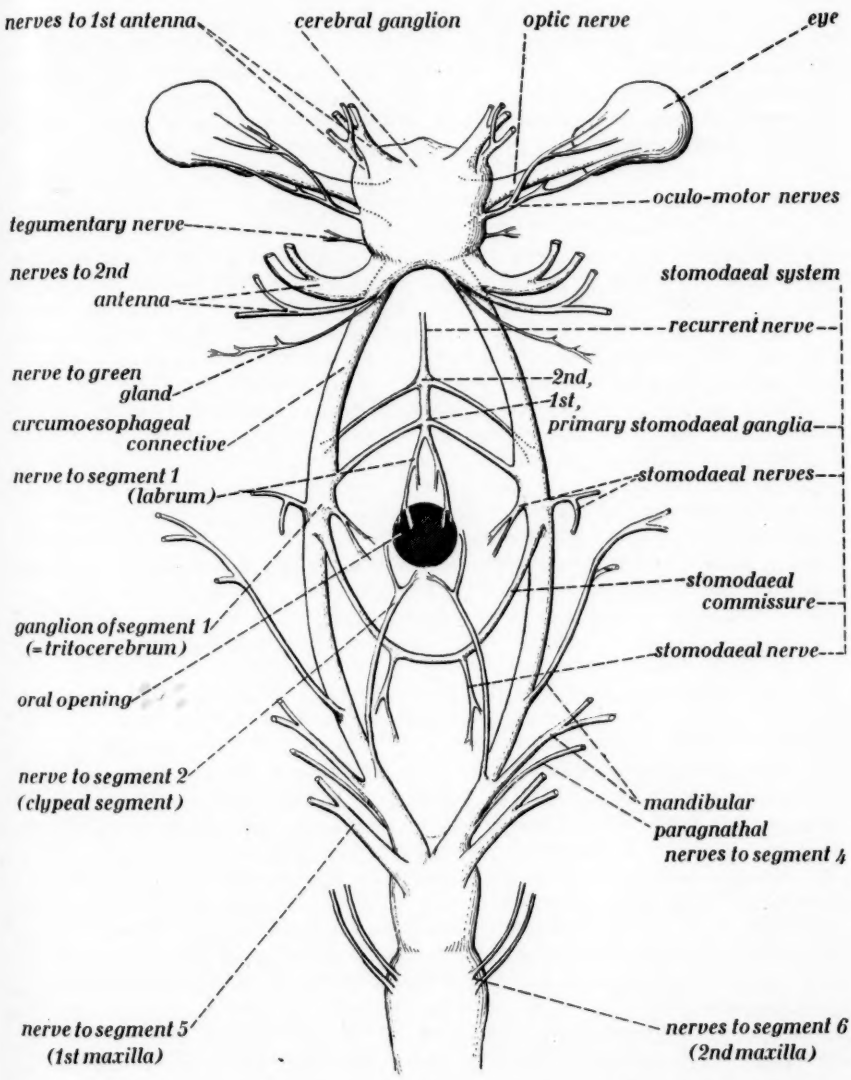

Fig. 3. *Palaemon paucidens*, cephalic nervous system ventral aspect (from Henry).

somites which are not represented in the definitive head and which may be compared with the telson or twelfth abdominal segment reported as commonly found in the embryo but which is not recognizably represented in the adult.

(c) *The clypeal and hypopharyngeal nerve*

In the Chilopoda and Crustacea studied by Henry a pair of nerves which originate from either the circumoesophageal connectives or the suboesophageal ganglion innervates the hypopharynx and certain muscles associated with the clypeal region. Henry homologizes these nerves with those of the "second

segment" in the Polychaeta which arise from a pair of ganglionic masses on the circumoesophageal connectives (fig. 2). She concludes from the distribution of these nerves that the clypeus and hypopharynx constitute the second head segment. This intrepretation of the hypopharynx is rather startling since embryologists generally have described its origin from the ventral region of one or more gnathal segments.

It will be found on examining Henry's figures that the roots of the hypopharyngeal or clypeal nerves, whether they originate from the connective or from the suboesophageal ganglion, are closely associated with the roots of the mandibular nerve and can quite as readily be interpreted as having their origin in the mandibular ganglion (figs. 3 and 4). In the decapod *Palaemon* (fig. 3) there are two widely separated mandibular nerves. The clypeal nerve arises at the same level as the posterior mandibular nerve; in other words its root lies nearer to the mandibular ganglion than does the root of the anterior mandibular nerve. Earlier in the same paper Henry (1948, p. 7) refers to a condition in *Apus* (fig. 4) where the second antennal nerve, a tegumentary nerve to the head capsule, and the tritocerebral ganglion have a spatial relationship similar to that of the anterior mandibular nerve, the clypeal nerve and mandibular ganglion in *Palaemon*. She argues that the tegumentary nerve does not originate in the tritocerebrum and therefore "to assume that the tritocerebrum is the source of the nerves to the second antennae" (which arise anterior to the tegumentary nerve) "demands a belief in segmental interchanging and criss-crossing of nerves that finds no support in any evidence yet presented". A sound principle, but surely the converse must also be true. If the clypeal nerve arises between the mandibular nerve and the mandibular ganglion it cannot, without "segmental interchanging and criss-crossing", belong to a neuromere which primitively lies two segments anterior to the mandibular neuromere. There is, therefore, strong evidence that the clypeal or hypopharyngeal nerve originates from the mandibular neuromere, which would be expected if, as generally claimed, the mandibular segment is the principal source of the hypopharynx.

If the hypopharyngeal nerve belongs to the mandibular segment, it is necessary to explain its association with the clypeus. In the Crustacea Henry describes the nerve as innervating "muscles which insert on the small dermal area immediately above and behind the labrum", i.e., the clypeal region. In the Chilopoda she described it as "innervating certain muscles which seem to belong to the clypeus". In neither case is anything known of the origin of these muscles. Henry assumes that because they are attached in the clypeal region they must belong to a clypeal segment, but the head of arthropods, like that of vertebrates, is a highly modified structure formed by the fusion of several segments, and it would not be surprising if in the one as in the other there has been some shift in the segmental relationships of the muscles. Indeed Wiesmann (1926) claims that in *Carausius morosus* an anterior portion of the mandibular sacs forms the antennal muscles.

(d) *The innervation of the labrum*

The tritocerebrum gives rise to the stomodaeal nervous system, therefore, Henry homologizes it with the ganglion of the first segment in the Annelida. Since it innervates the labrum she believes that the labrum is an independent segment homologous with the first segment of the Annelida. This theory will be discussed in the following section.

2. *Two Secondary Sclerites Forming Parts of a Single Segment*

Snodgrass, among contemporary workers, is the principal supporter of this theory which asserts that all that part of the head derived from the blastocephalon,

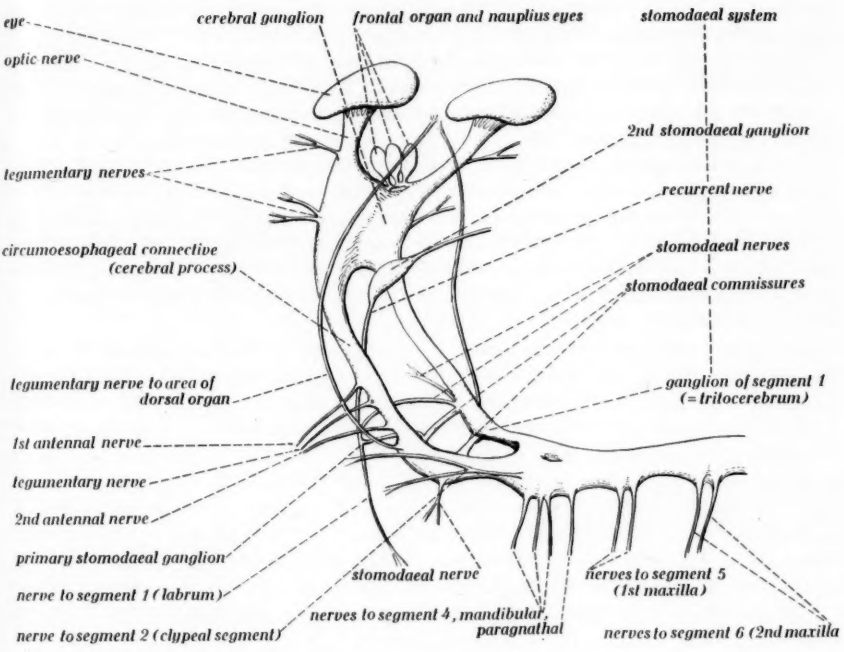

Fig. 4. *Apus longicaudatus*, cephalic nervous system lateral aspect (from Henry).

i.e., the labral, clypeal and occulo-antennal regions, constitutes a single segment, and any sutures therein are secondary, having no relation to primary intersegmental lines. He (1938) has advanced arguments to support this theory and other arguments are implicit in the earlier part of this discussion. If the blastocephalon or any part of it is derived from the annelidan prostomium, it must be derived from that of the Polychaeta with its eyes, antennae and palpi, i.e., the third segment according to Henry and not the first; consequently we should expect the blastocephalon to be composed of three segments. It is, therefore, necessary to consider whether Henry's theory of the proboscis invalidates the arguments in favour of the one-segment theory.

As stated earlier Henry regards the prostomium of the Oligochaeta as the homologue of the first segment of the polychaete proboscis. Unfortunately knowledge of the development of the Annelida is not very extensive and knowledge of the evolutionary history of the Oligochaeta still less so. It is usually assumed that the latter is an offshoot from the Polychaeta. Whether or not this is so there can be no doubt that the Oligochaeta and modern Polychaeta are derived from a common ancestral stock. If the prostomium of the Oligochaeta is the first segment of the Polychaeta the former group presumably split off from the common stock before the invagination of the anterior segments took place, otherwise we must assume that they have since undergone a process of reversed evolution.

There is, however, another possible explanation of segmentation in Oligochaeta still based on Henry's theory, and that is the partial or complete atrophy of the proboscis, leaving the head lobe as the anterior region. The most obvious

external difference between the two groups is the absence in Oligochaeta of salient structures such as parapodia, antennae, palpi and cirri. The absence of parapodia seems to be due to loss or reduction and the same may be true of other organs. Now in all of the Polychaeta studied by Henry the first segment is lost except for the jaws. In *Lumbrineris* and *Marphysa* the third segment is reduced except for the head lobe and in the latter the second segment also seems to be reduced. In addition *Lumbrineris* has lost its prostomial sense organs and its parapodia are reduced. There is obviously some tendency among the Polychaeta towards a reduction in the proboscis and appendages and this carried far enough would result in forms resembling the Oligochaeta in which the head lobe forms the most anterior region. With the loss of the anterior segments their ganglia would atrophy leaving the ganglion of the third segment as the anterior or cerebral ganglion.

The same reasoning may, of course, be applied to the insect head as far as the atrophy of the proboscis and its nerves is concerned. It is, therefore, not inconceivable that the blastocephalon in insects may represent a single annelid segment even if Henry's theory of the proboscis is accepted.

The argument just put forward is not to be regarded as a theory of annelid and arthropod evolution, but it suggests a possible alternative explanation and a field worthy of investigation. I can find nothing in Henry's figures which is inconsistent with it. Indeed she herself (Henry 1949) admits implicitly that there is no inherent impossibility in it when she asserts that in the scorpion *Uroctonus mordax* the second segment of the annelid has disappeared completely.

Her insistence on the presence of a labral segment is based largely on the relations of the stomodaeal system which she rightly regards as homologous throughout the annulates. In the Polychaeta this system is associated with the ganglion of the first segment and in the insects with the tritocerebrum. She therefore regards the tritocerebrum as the ganglion of a segment homologous with the first segment of the Polychaeta, and this segment can only be the labrum. She evidently considers that the stomodaeal system is derived from the first ganglion and therefore always associated with it. I have no information on the development of this system in the Annelida, but in insects it develops independently of the central nervous system and its connection with the latter seems to be secondary. There seems to be no valid reason why it should not make connection with whichever happens to be the most anterior ganglion of the definitive ventral chain.

Before there was any doubt of the identity of the "prostomium" in the Polychaeta and Oligochaeta I had reached the conclusion that the tritocerebrum is the homologue of the cerebral ganglion of the latter. On the assumption just stated both of these ganglia would be homologues of the third ganglion of the Polychaeta and the tritocerebrum would innervate those structures within its segment whose nerve supply has not been taken over by the protocerebrum and deutocerebrum, i.e., the sense organs of the labrum and any muscles which originate from the labrum, clypeus and frons. This might explain why Henry could find no ganglion or nerves in the Arthropoda which she could homologize with the ganglion of the third segment in the Polychaeta. Furthermore, with the disappearance of the first two ganglia the stomodaeal nervous system would naturally be associated with the third.

Henry claims that the tritocerebrum innervates the labrum only. Actually this ganglion sends nerves to the productor and reductor muscles of the labrum, the retractor of the mouth angles and to some dilator muscles of the foregut. These muscles all originate from the frons or the clypeus and there is no proof

that they develop from the mesoderm of a labral segment. The fact that the tritocerebrum innervates muscles which, judged by their anatomical arrangement, may belong to the clypeal and frontal regions can be interpreted with an equal degree of probability as indicating that these regions are parts of a single segment.

Further, there appears to be some evidence that the tritocerebrum sometimes innervates the posterior part of the occulo-antennal region. Snodgrass (1935) states that "in Acrididae a large tegumentary nerve arises clearly from the base of the tritocerebrum . . . and forks . . . into two branches distributed to the epidermis of the fastigial area between the compound eyes". Henry (1948) describes a tegumentary nerve in the Branchiopoda which in *Apus* (fig. 4) originates a short distance in front of the tritocerebrum. In *Branchinecta*, judging from her figure, the same nerve apparently arises from the tritocerebrum at about the same level as the stomodaeal nerve. This tegumentary nerve passes to the head capsule behind the eyes. She denies that this nerve belongs to the tritocerebrum but her denial seems to be based solely on her belief that this ganglion innervates the labrum only. Inspection of her figures certainly suggests that the nerve may belong to the tritocerebrum.

We may conclude therefore that there is not decisive proof that the occulo-antennal region, the clypeus and the labrum may not be parts of a single segment, the homologue of the prostomium in the Polychaeta. If the proboscis of the latter is an eversible portion of the foregut as commonly believed there can be no segments in front of this region. If, on the other hand, Ferris and Henry are correct in their interpretation of the Polychaete proboscis, they have not given incontrovertible proof that the two anterior segments persist in the insect head*.

D. The Postantennal Segment

The sequence of head appendages of the Crustacea is: first antennae, second antennae, mandibles, etc. There is convincing evidence that the first antennae, which correspond to the antennae of insects, have developed from prostomial sense organs, but it has been maintained on anatomical and embryological evidence that the second antennae are segmental appendages serially homologous with the mouthparts and the trunk appendages.

Insects have no appendages between the antennae and the mandibles, but many competent embryologists have described an evanescent postantennal or intercalary segment. It has been generally accepted that the tritocerebrum is the persistent neuromere of this segment which otherwise forms no recognizable portion of the definitive head.

This interpretation of the tritocerebrum seems to be based, not on the facts of embryogeny, but on an old concept of the brain. According to this concept the protocerebrum and deutocerebrum are neuromeres of the occular and antennal segments respectively, and the tritocerebrum, since it lies between the antennal and mandibular ganglia, must be the neuromere of a postantennal segment. Because of the convincing evidence that the protocerebrum and deutocerebrum are not segmental ganglia but nervous concentrations associated with the development of important sense organs, this explanation is no longer satisfactory and it is more likely, as stated earlier, that the tritocerebrum is the neuromere of the first head segment, whether we believe this to be the labrum or the entire blastocephalon.

Ferris and Henry both deny the presence of a second antennal segment in any arthropod and claim that the second antennae of Crustacea, like the first, are derived from prostomial sensory structures. Examination of Henry's figures

*The evidence for a clypeal segment is decidedly weak, that for a labral segment somewhat stronger. Another possibility, therefore, is that only one of the anterior polychaete segments has been lost

shows that in the Branchiopoda (fig. 4) the second antennal nerve (as well as the first) arises from the circumoesophageal connective in front of the tritocerebrum, while in the other Crustacea studied, it apparently arises from the cerebral ganglion (fig. 3). This certainly suggests that the second antennae are innervated from the proto-deutocerebral complex, which, in turn, suggests that they are prostomial organs. If we accept the contention of the embryologists that the second antennae are the appendages of a distinct segment, it would appear that the plan of the nervous system in insects is different from that in Crustacea since the ganglion that innervates the labrum and stomodaeum would not be the same in both classes—a conclusion that morphologists would be loth to accept. The problem needs further study.

E. Conclusions

Henry's interpretation of the morphology of the head is based entirely on her study of the nervous system and ignores conflicting evidence from embryology. It must be remembered, however, that it is not always easy to interpret embryological phenomena in insects. The interpretation of some acknowledged authority is likely to be followed by a host of lesser workers until some one, more original, advances a new interpretation. This, right or wrong, will have the desirable effect of stimulating a more critical examination of the evidence. Henry's contribution is a challenging one and should certainly have this effect on anatomical and embryological studies of the annulates. Whether or not her theories are eventually confirmed, she has shown how unsure are the foundations of some of our concepts of annulate morphology and her work, the general excellence of which I wish to stress, should stimulate a more critical examination of these foundations.

Henry's inferences from the evidence she presents are for the most part legitimate. She seems to have consistently applied the razor of Occam and her conclusions are the simplest and most direct that can be drawn from the evidence and her basic assumption; but the principle of parsimony does not provide proof and I have tried to indicate some alternative interpretations in order to draw attention to other possible evolutionary paths.

This theory of annulate morphology advanced by Ferris and Henry contradicts all previous work. There is no doubt that much of this work is old, inexact, incomplete and unconfirmed, but the concepts derived from it have become so fixed in the zoological literature that zoologists generally will be unwilling to accept the inferences drawn from this study of the topographical anatomy of the nervous system until some of the older concepts have been definitely disproved. Before this latest theory can be finally accepted it will be necessary: (1) to prove the validity of the basic assumption that a segmental nerve is never associated with any organ not derived from the segment to which the neuromere from which the nerve arises primitively belongs; (2) to determine, from histological or embryological evidence, the neuromeres which have given rise to nerves which leave the cord from a connective or from a compound ganglion; (3) to disprove the contention of embryologists that the prostomium of annelids is an unsegmented region which develops in a manner different from the metameres which form the trunk region.

Some Structural Features of the Face

A. The Frons

The frons is usually defined as that area of the occulo-antennal region contained between the "epicranial arms" and bounded ventrally by the clypeus. It has been shown, however, (DuPorte 1946, Snodgrass 1947) that the so-called

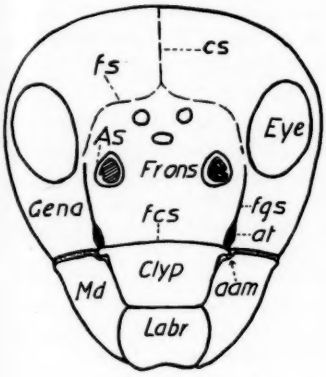

Figure 5

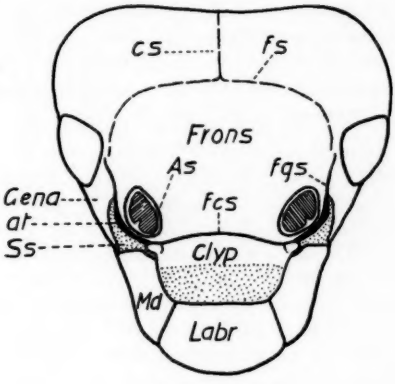

Figure 6

Fig. 5. Frontal view of the head in the generalized pterygote, schematic.
Fig. 6. *Anisolabis maritima*, frontal view of head.

"epicranial suture" is not, as usually described, an important morphological landmark and that it may be a composite structure having as its principal component the ecdysial line along which the larval cuticle splits at ecdysis. Since the arms of the ecdysial suture, i.e., the frontal suture, are extremely variable in position in different insects it was pointed out (DuPorte 1946) that a sclerite defined by the position of this suture can have no morphological significance and suggested instead that the frons should be defined as the median area between the two frontogenal sulci. These mark the junction of the primitive facial plate with the lateral parts of the cranium (the genae) when these descended ventrally so as to bring the two mandibular articulations into the same horizontal plane (Ferris 1942, DuPorte 1946). They apparently originate as inflections of the lateral edges of the primitive facial plate and the anterior tentorial arms are primitively associated with these inflections and not with the frontoclypeal as claimed by Snodgrass (1935).

The frons, as thus defined is not separated dorsally from the vertex. In those insects in which the frontal suture is present that part of it which would lie between the frontogenal sutures, if the ends of these were produced, may be regarded arbitrarily as forming the dorsal limit of the frons. Figure 5 shows the hypothetical structure of the generalized face, and the face of the earwig (fig. 6) resembles this very closely.

Snodgrass (1947) prefers to retain the old definition of the frons as the area enclosed by the frontal suture but admits that as thus defined it has no morphological significance. A changed concept of the frons will probably cause some confusion in the taxonomic literature but since the vast majority of adult insects have no frontal suture it is impossible anyway to determine the limits of the frons by this criterion.

B. The Clypeus

Ferris (1942) believes that the frontoclypeal suture is an intersegmental line but it seems more probable that it is a secondary suture marking the position of a functional inflection across a primitively single frontoclypeal sclerite. This inflection meets the need for greater strength and more precise leverage resulting from the establishment of the secondary articulations of the mandibles with the

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frontoclypeal sclerite (DuPorte, 1946). In most generalized insects it lies transversely across the face, terminating immediately dorsal to the mandibular articulations (Figs. 5, 6, fcs.). In this position it is at the level of the mouth and therefore cuts off a preoral clypeus from a postoral frons.

In many of the higher insects the apparent preoral region is greatly reduced; there is no transverse suture but, instead, an inverted U-shaped suture cutting off a sclerite which appears to extend dorsally, invading what was formerly the frontal area. This sclerite is generally called the clypeus and the suture is regarded as the frontoclypeal suture which has migrated dorsally (Snodgrass 1935). If the clypeus is a segment, as Ferris claims, there is no difficulty in accepting this view. If it is a secondary sclerite, a view which Snodgrass accepts, a shifting or migration dorsally of the functional ridge which separates it from the frons would no longer separate a postoral from a wholly preoral sclerite, and it is questionable whether the new sclerite should be called a clypeus rather than a frontoclypeus since the new position of the inflection would be across the original frons (DuPorte 1946). Snodgrass (1947) claims, however, that a clypeus of the type described is still preoral. Presumably the mouth accompanies the suture in its dorsal shift. I could not accept this view because I found it difficult to envisage a mechanism which would explain how the position of the mouth follows the peregrinations of a purely functional infolding of the integument.

Recently, however, while making a study of the head in the Hymenoptera, I found evidence which seems to provide a sort of compromise between Snodgrass' views and my own. This work was later turned over to one of my graduate students who, quite independently, and on slightly different evidence, reached the same conclusion (DuPorte and Bigelow, 1952). The evidence indicates that neither the frontoclypeal inflection nor the mouth has shifted its position, but that the genal and postgenal areas have continued their descent ventrally, the mesal edges of the genae fusing with the previously free lateral edges of the clypeus. At the same time the anterior articulations of the mandibles have also shifted ventrally following the similar shift in their posterior articulations so that the two still lie in the same horizontal plane. Comparison of fig. 7 with fig. 5 will make clear the relationship of the hymenopterous head with the generalized head. The frontogenal sutures (fgs), anterior tentorial pits (at) and the frontoclypeal suture (fcs) have the same relationships in both, but with the ventral extension of the genae in the hymenopteron and their fusion with the clypeus a pair of new sutures, the clypeogenal (cgs), has been established. The anterior articulation of the mandible has shifted from its primitive position (aam) to a more ventral position (aam'). The internal view of the face of the honey bee (fig. 8) shows the corresponding inflections or ridges.

The so-called "frontoclypeal suture" is therefore a compound suture. The transverse portion (fcs) is the true frontoclypeal suture, the portions containing the tentorial pits (at) belong to the frontogenal sutures (fgs) and the vertical portions are the clypeogenal sutures (cgs). The term "frontoclypeal suture" is therefore inapplicable to the complete U-shaped suture, but we suggest that the term "epistomal suture" be retained because of its somewhat less precise connotation.

If this theory of the clypeus is correct, there is now no difficulty in accepting Snodgrass' criteria for the identification of the clypeus. Our critical study, however, has been limited to the Hymenoptera, particularly the Symphyta, and the conclusions reached may not be entirely applicable to all insects with this type of face.

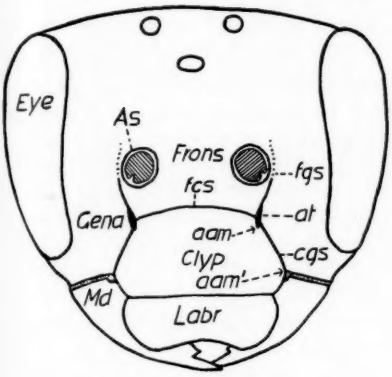

Figure 7

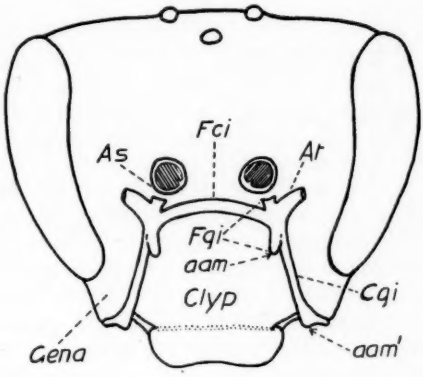

Figure 8

Fig. 7. Frontal view of head in a generalized Hymenopteron, schematic. (From DuPorte and Bigelow).

Fig. 8. *Apis mellifica*, worker. Internal aspect of face.

C. Use of the Term "Suture"

The term "suture", meaning literally "a seam", is borrowed from vertebrate anatomy where it is used to designate the immovable articulation of two independently ossified bones. It is used in other fields of biology to indicate the line of junction or of separation of two individual structures. In entomology, it is commonly used to designate the line of demarcation between sclerites, regardless of the method of its origin.

Snodgrass (1947) would restrict its use to those cases in which it forms a seam between two independent sclerites which have become secondarily united. Thus the line of demarcation between the frons and clypeus is a suture if these two sclerites are parts of separate segments, but it is not a suture if it represents the line of inflection in a primitively single sclerite. This is an unnecessary refinement in terminology since the term is used in a wider sense in other fields of biology and because it is not possible to identify a true suture by inspection. Whether the frontoclypeal groove is to be regarded as a true suture or not depends entirely on the interpretation of the morphology of the head.

Entomological orismology abounds in terms borrowed from vertebrate zoology because of some superficial resemblance or analogy between vertebrate and insect structures—terms which cannot possibly be used with their strict original meanings.

Using the term in its generally accepted sense, sutures are of two distinct kinds each formed in two different ways. *Line sutures* are narrow unsclerotized strips separating two sclerites. They may result, as in the ecdysial suture, from the non-sclerotization of a line in a primitively continuous plate. One of the definitions of a suture given by Henderson, Henderson and Kenneth (1949) is "a dehiscence line", which exactly describes the ecdysial suture. A line suture may also separate two independent sclerites which approach each other closely without fusing.

A *sulcus* or *groove suture* is an external groove which marks the position of an inflection or internal ridge. This ridge, as in the frontoclypeal inflection, may be formed by the infolding of a primitively single sclerite or, as in the frontogenal inflection, by the fusion of two independent sclerites.

Summary

Based on studies of the nervous system in the annulates, and assuming that the nerves of a segmental ganglion are restricted to organs which primitively belong to that segment, Henry claims (1) that the proboscis of the Polychaeta consists of three segments, the prostomium being a dorsal head lobe of the third; (2) that the prostomium of the Oligochaeta is the first segment and, therefore, not homologous with that of the Polychaeta; (3) that the head of insects and most other arthropods includes the three segments of the polychaete proboscis, these being represented by the labrum, clypeus and occulo-antennal region; (4) that the hypopharynx is the ventral region of the second segment; (5) that there is no evidence of a second antennal segment in any arthropod.

As against Henry's claims it is contended (1) that some of her observations are susceptible to other interpretations; (2) that the evidence for regarding the occulo-antennal region, the clypeus and the labrum as parts of a single segment are at least as strong as that for regarding them as three distinct segments; (3) that evidence from the nervous system is not sufficient to determine the segmentation of the head; (4) that much more evidence from embryology and morphology is needed before a final decision can be made on Henry's claims.

In a discussion of some structures of the definitive head it was pointed out (1) that the frontal suture does not define the same region of the head in all insects and that it is absent from the heads of most adult insects; (2) that the frontogenal sutures are a better criterion for defining the frons; (3) that in the Hymenoptera, where the clypeus has apparently extended dorsally into the frontal region, the true explanation is that the frontoclypeal suture retains its primitive position but the genae have descended ventrally, their mesal edges fusing with the lateral edges of the clypeus; (4) that there is no need to depart from the current usage as applied to the term "suture".

Acknowledgment

I wish to acknowledge the courtesy of Professor C. F. Ferris and Dr. Laura Henry in permitting me to use three of Dr. Henry's original drawings.

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Abbreviations

aam—primtive position of the anterior mandibular articulation in the generalized pterygote.
aam′—secondary position of the anterior mandibular articulation in Hymenoptera.

As—antennal socket.	Clyp—clypeus.	fgs—frontogenal suture.
At—anterior tentorial arm.	cs—coronal suture.	fs—frontal suture.
at—anterior tentorial pit.	Fci—frontoclypeal inflection.	Labr—labrum.
Cgi—clypeogenal inflection.	fcs—frontoclypeal suture.	Md—mandible.
cgs—clypeogenal suture.	Fgi—frontogenal inflection.	Ss—subocular sinus.

Observations on Two Species of Pseudoscorpions

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Introduction

Very few papers have been published on the life history of pseudoscorpions. The literature has been summarized by Kästner (1927), J. C. Chamberlin (1931), Beier (1932) and Roewer (1936-1940). The following contributions are based upon observation of two species of pseudoscorpions which were kept in captivity.

I should like to give sincere thanks to Dr. J. C. Chamberlin for reading the paper and giving valuable suggestions, to Dr. C. C. Hoff for determining the chernetid pseudoscorpions, to Mrs. Rosalie Rogers Talbert for assistance in maintaining and feeding the pseudoscorpions; and to my wife who has aided in the work.

Notes on *Chelifer cancroides*

Chelifer cancroides (Linn.), a nearly cosmopolitan species, was collected in Madison, Wisconsin, in houses. Most were found on walls or stranded, unable to escape, on smooth surfaces such as bathtubs. But, others were found under various conditions: several in laundry, one in a bed, another with a telephone bill, and one on a loaf of bread. Two were found with *Lamprochernes minor* in the manure pile mentioned below. The animals were found during all seasons in Madison, but more were taken in April and early May than in other months. Though the natural means of dispersion of pseudoscorpions is said to be phoresy (Roewer, 1936-1940, Vachon 1940, 1947, Beier 1948), only one probable instance was recorded: one *Chelifer* which was brought in was reported to have been found in a bathroom, attached to a silverfish.

Of about 85 *Chelifer cancroides* collected in Madison, the sex ratio observed was about three females to one male. The reason for this is not at all clear. The nymphs, unfortunately, can not be sexed. The number of captive nymphs that reached adulthood was not large enough to justify definite conclusions, though the sex ratio of these animals appeared to be equal.

Chelifer cancroides in captivity was kept isolated in screw-cap vials, 65 mm. in length, containing a rectangular piece of paper about as long and wide as the space within the vial.

Feeding has been described in detail by Kästner (1931). It is assumed that under natural conditions, *Chelifer* feeds on small animals found in houses. No particular insect abundance has been associated with *Chelifer* in Madison. It is not surprising, therefore, to notice that most of the *Chelifer* collected were emaciated.

In the laboratory, pseudoscorpions were given various foods depending on their size: the smallest received collembolans and booklice; the larger animals

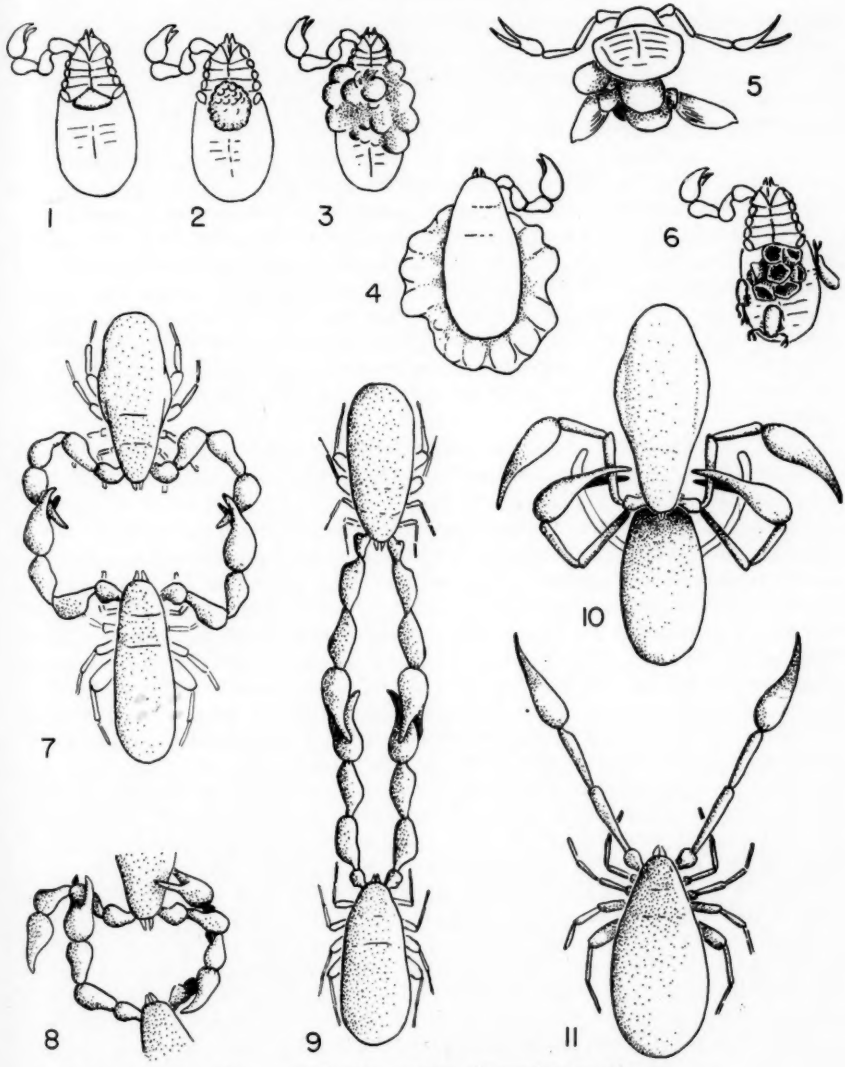
and adults were given larvae of the cucujid grain beetle, *Laemophloeus ferrugineus* (Steph.). When those were not available, Drosophila adults or larvae of the confused flour beetle (*Tribolium confusum* Duval) were substituted. (Schlottke, 1940, mentions that *Chelifer cancroides* he raised in Germany refused Drosophila). First instars were fed daily, but adults did not need food more than once weekly. Laboratory reared specimens appeared better fed than those collected in the wild; however, they were somewhat smaller in size.

The behaviour of pseudoscorpions is of interest because, though they are predators, some species like *Lamprochernes minor*, may be quite gregarious. Even *Chelifer cancroides* may at times be very abundant in a small area (Frickhinger 1919). In discussing behavior it should be kept in mind that though *Chelifer cancroides* has two eyes, its vision is probably poor. Pseudoscorpions have, on their pedipalps, long tactile setae which correspond to similar setae on spiders (Roewer). During the following observations, the animals were confined in vials or petri dishes, and were studied under ordinary conditions of light. While the animals did not avoid light, they seemed to be thigmotactic.

The behavior as here observed differs for the two sexes of *C. cancroides*. If two females were placed together, it was usual for one of them to stretch one pedipalp rigidly forward, waving it relatively slowly in a direction lateral upwards, then mesad downwards (fig. 11). (On occasion a male was seen to wave a palp at another individual, however this movement was observed only in contact between Chelifers). Usually the other female retreated, frequently by turning to one side and running away. In case of other kinds of disturbance, the pseudoscorpion usually did not turn about, but faced the disturbance and then rapidly ran backwards. In one observation, both females waved their pedipalps and ran toward each other. There was some fencing with the palps before the smaller one turned around and moved away.

Though there are descriptions of it in the literature, mating behavior is very difficult to observe in *Chelifer cancroides*. Despite many attempts at mating two animals, the complete process was observed only twice, in both instances with females that had been raised in captivity. This possibly gives further support to the belief that *Chelifer* will mate only once. If that is so, it may be that the females collected in the Madison area all had had a mating experience before they came into capitvity, a point which is of interest because of the apparent scarcity of males.

Adult males were not always ready to mate; however, this lack of readiness could not be correlated with either the age of the individual or the season. A male *Chelifer* that was ready for mating would, immediately on seeing a female, pull back his pedipalps and vibrate his abdomen rapidly from side to side. Simultaneously with the vibration, the "ramshorn organs" were extruded. (The ramshorn organs lie contracted under the genital plates in the few species belonging to the Cheliferinae). These two structures rod-like in appearance, are evaginated in sexual display (fig. 10). The unreceptive female reacted by waving her pedipalps and then moving away, sometimes taking a route passing directly over the male. After her departure, the male would cease vibrating his abdomen and pull in the "ramshorn organs". As the male perceived the female passing by, he vibrated his abdomen and protruded the organs again. Only once were the "ramshorn organs" observed under high power dissecting microscope while withdrawing. The ends seemed to shrivel up slightly and the rest seemed to pull in as smoothly as if they were highly polished metal rods. When a female was receptive, she did not run away, but seemed to encourage the male by waving her pedipalps and wiggling her abdomen. In general, the mating of *Chelifer*



1. *Lamprochernes minor*, ventral view, earliest observed stage of eggs.
2. *Lamprochernes minor*, ventral view, several days later.
3. *Lamprochernes minor*, ventral view, eggs midway in development.
4. *Lamprochernes minor*, dorsal view, two to three days before emergence of the protonymphs.
5. *Chelifer cancroides*, viewed from behind, protonymphs emerging from brood sac.
6. *Pselaphochernes parvus* Hoff, 1945, (a chernetid pseudoscorpion) ventral view, residua of brood sac and three protonymphs climbing over the mother.
7. *Lamprochernes minor*, mating position. The male is holding the female.
8. *Lamprochernes minor*, a temporary hold during mating.
9. *Lamprochernes minor*, mating position before breaking apart.
10. *Chelifer cancroides*, mating position. The male is holding the female.
11. *Chelifer cancroides* female, "recognizing" another female.

Fig. 1-4 drawings made from different individuals. Some appendages have been removed from fig. 1-6, 10 and 11.

followed Vachon's (1938) description, but was somewhat less diagrammatic and less elaborate.

In order to find out whether or not the males would recognize the sex of another individual of the species, two males were placed together. One of them immediately started vibrating his abdomen and extruded the "ramshorn organs". The other animal ran away, followed by the excited male, who as he approached the fleeing individual, started vibrating his abdomen. The experiment was repeated with the aggressive male of the previous observation and another male. The first individual again displayed: however, the new male ignored him, walking right over and past him. At another meeting of these two individuals, the new male started fencing with the pedipalps. Each one of these two males was now placed, in turn with the same female, which gave the usual sign of waving her palps. The less aggressive of the two males did not show any interest and ignored the female. The aggressive male, however, immediately started vibrating his abdomen, at which the female waved her pedipalp, then turned and moved away.

Chelifer was observed to have usually only one litter a year. The exception was one which, after losing its first brood-sac, succeeded in producing a litter several months later.

The actual extrusion of eggs was not seen. During the growth of the embryos, the eggs, covered collectively by a thin membranous brood-sac, appeared slowly to decrease in number, while the remaining eggs increased rapidly in size (fig. 1-4). The development has been described in detail by Vachon (1938) and in a recent paper by Janetschek. According to these authors, the newly hatched larvae attach themselves by means of their sucking beaks to their mother's genital orifice through which they are fed on a kind of uterine milk secreted by her transformed ovaries. During this feeding period, the parent becomes quite emaciated. After a time, the larvae moult and leave the brood-sac. The emergence as here observed in both *Chelifer* and *Lamprochernes minor* Hoff was reminiscent of the moult. The head of the young animal was directed outward and the exuviae slipped back, eventually to shrivel up as in a moult. The newly emerged nymph stayed attached to the mother by its posterior end for several hours, apparently until the appendages became sufficiently dry to support their owner (fig. 5). While the legs and pedipalps dried, they were brought from their folded ventral position into a hanging position, and then were brought forward. Some rhythmic contractions in the body of the young were observed during this time. When dry, the nymphs seemed to break away from the parent. The residua, which looks like the cells of the paper wasps' nest, stayed attached to the mother for another day or two. The young in the meanwhile climbed all over the mother and even attached themselves with their chelicerae to parts of her body, hitch-hiking around with her for several days (fig. 6). The young of *Chelifer cancroides* (which species makes a nesting chamber), stayed in the nest until the mother made a hole big enough for them to get out. Pseudoscorpions have three instars before the adult state is reached. *Chelifer* matured in the laboratory in from four and one half to fourteen months. Notes on the early instars have been published in an earlier paper (Levi, 1948).

It was possible to age adults of *Chelifer* roughly by their ability to walk on the underside of a glass surface. Recently moulted adult Chelifers had no difficulty walking on glass, while old pseudoscorpions and occasionally those in a moribund condition could not walk on glass at all. The oldest *Chelifer* in this study lived two years. This animal was kept at room temperature at all times. A female *Chelifer cancroides* by Schlottke lived five years. Schlottke, however,

had to chill his animals during the winter months, as they refused food during this season and soon starved at room temperatures. Our pseudoscorpions did not display this behavior. Schlottke found that unmated female *Chelifer* died much earlier than males or mated females. He gives the average life of males and females as two and one-half years after reaching sexual maturity at one or two years of age.

Notes on *Lamprochernes minor*

Lamprochernes minor Hoff, 1949, was first found on the bark of cottonwood logs outside of Madison, Wisconsin. Unfortunately, its collection resulted in the destruction of the habitat. A manure pile at an abandoned farm in Madison proved to contain an abundance of pseudoscorpions. The animals were found on the undersides of timbers and roofing material that lay on the manure. Even the manure itself, when shaken through a sieve, yielded pseudoscorpions. In fall when the manure became drier, the pseudoscorpions seemed to disappear. Unfortunately the area was plowed up early in 1950, so that it was impossible to locate any further animals.

Chernetid pseudoscorpions, of which *Lamprochernes* is an example, are difficult to keep, and to my knowledge have never before been reared in captivity in such a way that they could be observed. Here they were kept in screw-cap vials 45 mm. long, containing a piece of paper. In turn the vials were kept in a desiccator jar having a saturated solution of potassium bisulfate in the lower compartment. The potassium bisulfate solution keeps the relative humidity between 80 and 90%; a higher humidity caused excessive growth of mould, while the pseudoscorpions did not survive at a lower one. The desiccator jars were kept darkened.

Lamprochernes does not seem to be very specific in its feeding habits, for many small insects served it as food. They were rarely feeding when collected. In captivity they were fed like *Chelifer cancroides*.

The behavior of *Lamprochernes* was observed under similar conditions as *C. cancroides*. It should be remembered that *Lamprochernes* does not have any eyes at all.

The behavior of this species (likewise the percentage of survival in captivity) differed for the two collecting sites. There is a possibility that we are dealing with different, though closely related species. However no morphological differences between the two groups could be found.

No special movements were observed when two females were brought together; the two animals seemed completely to ignore each other. No case of cannibalistic attack was observed either. It might be mentioned here that these animals fed much less readily than *Chelifer* and were rather slow to attack prey.

In spring, at least (experiments were not made during other seasons), males seemed always ready to mate, and all females appeared receptive. If males of *Lamprochernes* collected from the cottonwood log came close to a female, they would, with their pedipalps, seize those of the female (fig. 7) and start jerking her about. The female never resisted. At times the female would grasp a male first. If that occurred, the male would, in a short while change his position in such a way that he would hold the female. Schtschelkanowzeff (1910), according to Roewer, reports that the female of a Russian chernetid takes the initiative in mating. The accuracy of this observation has been doubted, in as much as the early observations on *Chelifer cancroides* by Kew (1912) and the more recent ones by Vachon (1938) do not agree with Schtschelkanowzeff. Since there is probably considerable variation in the mating behavior of different

pseudoscorpion species and since there is a tendency in *Lamprochernes minor* for the female to initiate mating, it may well be possible that the Russian author after all did not confuse the sexes of his animals as his critics suspected.

As soon as the male had gotten hold of the female, he would start jerking her pedipalps while at the same time moving slowly forward and backward with her. Before moving forward, the male was observed to tap the ground with the first pair of legs. The female held her abdomen very high and once a pumping movement was observed in the abdomen of a mating female. One particular male jumped off the ground each time he pulled the female back. Sometimes they lost their grip and would get a temporary new one, which might be like the one shown in fig. 8. Once it was observed that the pedipalps were crossed for a short time. Several times one of the females was first discovered by her partner while she was walking on the glass above him, and was jerked upside down. Usually after a minute or two, the grasp and the position were changed to the usual mating position. It is assumed that in walking forward the male deposits a spermatophore which is picked up by the female when she is pulled back by the male. However, this was never observed. The jerking decreased in intensity after about five minutes. Sometimes at this stage one of the pedipalps lost grip and would be held stretched out and vibrating. In a short while the pair would resume their holds and would stay quietly that way for ten minutes, jerking once in a while. After that the animals slowly stretched their pedipalps until they were in the position shown in fig. 9. In this position they remained for three quarters of an hour to an hour, after which they parted, only to join again next time they met. Usually, the following matings were less active and of shorter duration.

The *Lamprochernes* collected in the manure pile, though as far as could be told were of the same species, behaved slightly differently when mating. The male did not grasp the female immediately, but first, upon recognizing another pseudoscorpion, stretched out his pedipalps, vibrating them very rapidly up and down while strutting about. The females observed did not move away, but let themselves be grasped after a minute or two or even longer.

It was possible in only a few cases to bring two males together. In the case of animals from the cottonwood log, one male immediately took hold of the pedipalps of the other and started jerking. After a short time the second male pulled himself loose from the hold and ran away. At another meeting there was some fencing with the pedipalps. When males from the manure were placed together one of them started vibrating his stretched out pedipalp at the partner, which thereupon ran away.

In one observation, a female was placed with two males (all three animals came from the manure pile). One male started mating with the female while the other male walked by very closely to the pair but showed no change in behavior. Later after the parting of the mating animals, the unmated male vibrated his pedipalps at the mated male which ran away, then later waved at the female with which he then mated. The female in the couple of hours of observation, seemed to mate alternately with the two males. The unpaired male was never seen to display at the mating pair or to disturb them in any way. The female involved in the last observations was seen to vibrate her palps once or twice.

The life history of *Lamprochernes* resembles that of *Chelifer cancroides*. *Lamprochernes minor* differs from *Chelifer*, however, in that the animals under observation did not construct nests while carrying a brood-sac. The interval

between the first observation of eggs and the emergence of the young from the brood-sac was from 15 to 25 days. The number of young per litter was higher for *Lamprochernes* than for *Chelifer*, the four litters observed ranging from eleven to twenty-four. Some individuals carrying brood-sacs lost them. The actual loss was observed only once when an animal, apparently excited under a microscope light, squeezed between paper and glass, and was separated from its eggs. One animal, collected May 4, 1948, was seen to have eggs on May 24. Nymphs emerged successfully on June 17. On August 21, eggs were seen again; on August 26, they seemed larger but they disappeared by August 29. The third brood-sac, first observed on September 4, emerged on September 21. The last eggs of that particular pseudoscorpion were observed on July 2, 1949, but disappeared. The animals died in January, 1950.

Lamprochernes matured in four to six months. Data on the length of individual instars of *Lamprochernes* have been recorded, (Levi, 1949).

Of 120 *Lamprochernes* collected in the manure pile in April and May 1949, no immature stages were found. The sex ratio was equal. In fall collecting, both deutonymphs and tritonymphs were found. Protonymphs may have been overlooked because of their small size. There is the possibility that some survive the winter as nymphs, moulting early in spring to become adults. Others probably mature by the end of summer. *Lamprochernes* found in the cottonwood log during the winter were not using a hibernation nest. One animal collected as an adult lived for one year and eight months in captivity at room temperature and was at least two and a half years old at the time it died.

Causes of Death

The greatest mortality of both pseudoscorpion species appeared to be in the younger instars. Many of the protonymphs never took food and died of starvation. Most other deaths seemed to be connected with some moulting difficulty. It appeared that protonymphs whose moulting date was near the median moulting date of the group survived better than the animals moulting on the earliest or latest dates. A number of times it was observed that an animal was apparently ready to moult but did not succeed in initiating the process. In some cases animals which had already made chambers left them again; these individuals died shortly. Death during actual moulting seems quite rare. No cases were observed in which a pseudoscorpion had difficulty in emerging from its skin.

As can be inferred from their reproductive potential, pseudoscorpions have few enemies, though moulting pseudoscorpions are easy prey for any predator. No parasites were observed. Starvation, and possibly desiccation, seemed to act as population controls for *Chelifer cancroides*. *Lamprochernes*, on the other hand was found in areas of abundant food, and was rarely found in a starved condition. However, any small accident seemed to cause death. In the laboratory accidents involving separation of a limb or a part of a limb in either species usually resulted in death within several hours, with symptoms similar to those of desiccation. A notable exception was one female *Chelifer* which lost the most distal segment of one pedipalp when she was collected, but survived the handicap for almost a year. Only one abnormality was observed; an adult female *Chelifer*, apparently in excellent health, had an extra segment between the fourth and fifth tergite on the left side. The sternites appeared normal. With (1905) and Kästner (1927) have described abnormalities in segmentation in other species of pseudoscorpions.

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Regional Societies

On November 27th, 1952 the Entomological Society of Alberta was founded with executive officers as follows: President, E. H. Strickland; Vice-President, R. H. Painter; Secretary, L. A. Jacobson; Treasurer, G. A. Hobbs; Editor Librarian, R. W. Salt; Directors, H. Hurtig, W. C. McGuffin, T. Kilduff; Regional Director Entomological Society of Canada, R. W. Salt; Nominal Past President, C. W. Farstad. By the beginning of November 38 members had been enrolled in the new Society.

The Entomological Society of Saskatchewan was founded on November 5th, 1952, with executive officers as follows: President, L. G. Putnam; Vice-President, C. E. Brown; Secretary-Treasurer, M. N. MacLeod.

The third annual meeting of the reorganized Acadian Entomological Society was held April 15th and 16th at the new Science Service Laboratory, Kentville, N.S. The meeting featured discussions on animal population studies. Principal papers were contributed by A. D. Pickett, Dr. R. F. Morris, Dr. R. E. Balch, J. B. Adams and C. A. Miller. Discussion leaders included D. D. Pond, F. M. Cannon, Ray F. Morris, C. J. S. Fox, F. T. Lord and C. W. Maxwell. On the evening of April 16th a banquet was held at the Paramount Hotel in Wolfville. The guest speaker was A. Kelsall, who drew freely from his store of experience and gave a very interesting account of early entomology in the Maritime Provinces. A guided tour of historic sites in the Annapolis Valley was arranged by the President, A. D. Pickett.

Amino Acids in Insects[1]

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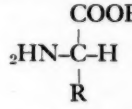
Institut de Biologie générale et de Zoologie
Université de Montréal

The object of this paper is to summarize some of the latest research work that has been done concerning the amino acids in insects and especially the research work in which I have collaborated.

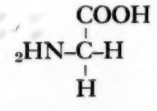
The Amino Acid Molecule

An amino acid is an organic compound which contains a grouping with acidic properties. Such a grouping in organic compounds is the carboxyl group. $-C(=O)-OH$, which may break or dissociate to give off hydrogen ions ($-COO^-$ and H^+). An amino acid, as implied from its name, contains also an amino group NH_2, that is very important for living beings because of its nitrogen. The general formula of an amino acid may be represented as follows:

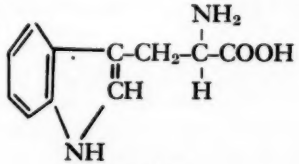


An organic compound with a carboxyl group, and an amino group usually on the second carbon, or alpha carbon.

The radical designated by R in the amino acid molecule represents the remainder of the molecule and may be equal to H, such as in the simplest amino acid glycine, or it may be a complex structure such as the indol ring in the important amino acid called tryptophan.



Glycine



Tryptophan

Amino acids are very important biologically. As a matter of fact, they are constituents of all living beings, plants and animals. In living matter, amino acid molecules can exist as free molecules in liquids such as blood, plant juice, but more often, hundreds of amino acid molecules combine chemically with each other to build up huge molecules of proteins which constitute the basic physico-chemical structure of living matter. The human body for instance is made up of about 15% proteins, or several pounds of amino acids. From 20 to 23 different amino acids have been isolated from proteins.

Amino Acids in Insect Blood

Insect blood contains an unusually high concentration of free amino acids in solution. Compared with human blood, the concentration of free amino acids in insect blood is from 20 to 100 times higher.

Until recent years, owing to the lack of adequate micromethods for amino acid analysis, it was very difficult if not impossible to determine the concentration of each amino acid in insect blood. There exist at present micromethods by means of which one can determine qualitatively and quantitatively the amino acids of insect blood. Such micromethods include microbiological assays and

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[1]Presented as an invitation paper at the 1st Annual Meeting of the Entomological Society of Canada and the 88th Annual Meeting of the Entomological Society of Ontario, at Ottawa on November 1, 1951.

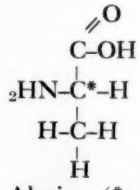
[2]Assistant Professor of Physiology.

paper partition chromatography. We have been using the latter method extensively in the past five years for the study of amino acids in insects (10). The results have shown that insect blood contains usually from 15 to 20 and possibly more, different free amino acids, including those not encountered in protein molecules, such as beta-alanine, taurine and alpho-amino-*n*-butyric acid.

In the past two years, with the development of a fairly accurate quantitative method of paper chromatography (2), we have made quantitative measurements of the concentration of each amino acid in insect blood. The insect used was the greater waxmouth, *Galleria mellonella*. It was observed that the total quantity and the concentration of most amino acids and amides in the blood of this species increase rather steadily during larval growth and reach a peak at the last larval instar. The concentration of the amino acids falls off slightly during the spinning of the cocoon, to increase again slightly in the pupa and finally decrease considerably down to a low concentration in the adult stage. These changes in amino acid concentration during growth and development vary somewhat with each amino acid. They may be more important for some amino compounds than for others, and they may also be insignificant for a few amino acids. Some amino acids such as hydroxy-proline and taurine may appear at metamorphosis. From preliminary analytical results with an insect having complete metamorphosis, it appears that a portion of the amino acids taken from the food is accumulated in the blood during larval growth as reserve material used for the building up of the cocoon proteins and of the adult tissues during metamorphosis. In other words, many amino acids would be material stored into the blood and utilized later during periods when there is little or no feeding but when the metabolic activities are high, as, for example, during metamorphosis and reproduction.

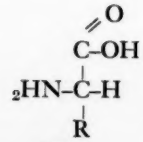
Stereoisomers

Referring back to the general amino acid formula or to the structure of alanine, one observes that in such a structure there exists one asymmetrical carbon atom, that is to say, a carbon atom carrying four atoms or groups of atoms different from each other.

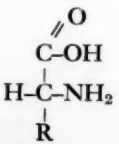


Alanine (*asymmetric carbon)

Because of the presence of this asymmetrical carbon atom, there may be two stereoisomers of each amino acid, depending on the position in space of the amino group. This rule applies to all amino acids except glycine. The two isomers of an amino acid may be shown as follows:



L form



D form

All the amino acids with the exception of glycine can exist either as the L or the D form, depending on the position of the amino group around the carbon atom, either left or right of the carbon chain. The L and D forms of each amino acid have the same chemical properties and the same molecular composition. They differ however in the extent to which they rotate plane polarized light.

In living beings, in 99.99% of the cases studied, amino acids that are found free or in the protein molecules are of the L form. This is rather interesting. It is not known why living matter is made up almost exclusively of L isomers, when we know that L and D isomers have the same chemical properties. One possible explanation is that the enzymes catalysing amino acid synthesis in living organisms catalyse only the formation of L-amino acids. Many enzymes are peculiar in their specific action toward a particular isomer of a compound.

We have been wondering if in insect blood amino acids are always of the L or natural configuration. After having developed a micromethod for the determination of D and L isomers of amino acids (4), studies were made on three insect species, namely: an Hemipteron, the milkweed bug, *Oncopeltus fasciatus*, a Coleopteron, the Mexican bean beetle, *Epilachna varivestis*, and a Lepidopteron, the southern armyworm, *Prodenia eridania*. To our surprise, the unnatural or D form of alanine was identified in the blood of the adult milkweed bug, *Oncopeltus fasciatus*. The reason of the presence of this extremely rare isomer of alanine in the blood of that insect is not known. Analyses of the food (milkweed seeds and water), on which this insect was reared revealed that it does not contain D-alanine. It is therefore concluded that this unnatural isomer of alanine is formed within the insect, either by microorganisms or during the intermediary metabolism.

Deamination in Insects

When the proteins of the food are hydrolysed in the digestive tract of mammals, free amino acids are liberated and absorbed. They pass through the wall of the digestive tract into the blood and they are carried to all the tissues where they are utilised for various needs, especially for the synthesis of tissue proteins. Part of the absorbed amino acids passing through the liver and the kidneys are deaminated. The amino group of their molecule is removed to yield a keto acid and ammonia. Deamination in the liver and kidney is catalysed by several enzymes called deaminases. The two most important ones are L-amino acid oxidase which deaminates and oxidizes the majority of L-amino acids and D-amino acid oxidase which deaminates and oxidizes the majority of D-amino acids that may be present.

Several series of experiments with different insect tissues showed a rather high deaminase activity in the fat body of the American roach, *Periplaneta americana*. As in the liver of mammals, the fat body of this insect showed a high D-amino acid oxidase activity and a very low L-amino acid oxidase activity. In other words, when the fat body of that insect was incubated with amino acid solutions, most D and DL-amino acids were deaminated rapidly, whereas L-amino acids were deaminated very slowly or not at all. A low but significant deaminase activity was found also in the Malpighian tubules of the same insect species (1). From the results of other experiments made with antiseptic substances, we are inclined to believe that deamination, as it occurs in the fat body and Malpighian tubules of the American roach, is due to the presence of microorganisms in these organs, possibly intracellular symbionts, which are apparently always present in the fat body of the American roach. It is known also that several kinds of

microorganisms (Bacteria, Protozoa, etc.) are normally found in the alimentary tract of the American roach and it is possible that many of these microorganisms find their way into the Malpighian tubules.

The tissues of a few other insect species were also examined for deaminase activity. D-amino acid oxidase activity was apparent from the fat body of the greater waxmoth larva, *Galleria mellonella*, of the German cockroach, *Blatella germanica*, and in the Malpighian tubules of the latter species.

No D-amino acid oxidase activity was detected in the fat body or Malpighian tubules of adults of the milkweed bug, *Oncopeltus fasciatus*. This negative result agrees well with the presence of D-alanine in the blood of that insect. (4)

Amino Acids in Insect Nutrition

As mentioned in the beginning of this paper, amino acids are present in all living organisms, where they form the protein molecules. Young growing animals, rapidly increasing in size and weight, are in constant need for more and more amino acids for the building up of new tissue proteins. Many amino acids can be synthesized by the growing animal. Other amino acids cannot be synthesized by the growing animal and finally some can be synthesized but not at a rate rapid enough to satisfy the needs of the growing animal. The animal must receive from an external source the amino acids that he cannot synthesize and this external source is the food.

There is for each animal species, from the Protozoa up to the Mammals, with very few exceptions, one or most often a number of amino acids essential or indispensable in the diet for a normal growth and maintenance of the animal.

Insects are no exception to this rule. Several workers have shown that a number of amino acids are essential in the diet of insects for normal growth and development. For instance, House (6) working under aseptic conditions with chemically defined diets, was able to demonstrate that out of seven amino acids assayed, five were essential for the normal growth and/or development of *Blatella germanica*. These five essential amino acids are: Valine, tryptophan, arginine, histidine and very probably cystine. Golberg and DeMeillon have found that mosquito larvae of *Aedes aegypti* require ten essential amino acids (5). Lemonde and Bernard, in a work published recently (7), have showed that larvae of *Tribolium confusum* require in their diet at least ten essential amino acids which are: Threonine, valine, leucine, isoleucine, arginine, lysine, methionine, phenylalanine, histidine and tryptophan.

In *Tribolium confusum*, if one of these essential amino acids, lysine for instance, is completely lacking from the diet of the larvae, the length of the pupal stage is doubled (instead of being 30 days as in ordinary experimental conditions, it lasts about 60 days). If only one of the following essential amino acids is lacking: Valine, histidine, tryptophan or leucine, pupation does not occur and there is no metamorphosis. From these results and others published in the literature, we can draw a conclusion that eventually will be applied to most insects. Insects must receive from their food a number of essential amino acids and each essential amino acid must be provided in a definite minimum amount daily for a rapid rate of growth, development and reproduction.

The interesting problem of plant resistance to insects can be considered at this point. For a number of years, at the Science Service Laboratory, at St-Jean, Qué., a research project has been directed by Mr. J. B. Maltais on the causes of plant resistance to insects. Through his work, it has been established that there exists a relative resistance between different varieties of peas toward pea aphid

attacks (8). Under natural field conditions and also in replicated plots, certain pea varieties will always or almost always carry a much lower aphid population than others. For instance, when one plant of the garden pea Champion of England carries ten aphids, one plant of the variety Perfection will usually carry 80 to 100 aphids or more.

From preliminary nitrogen analyses of such varieties, using the Kjeldahl method, it was found by Maltais (9) that resistant varieties contain less soluble nitrogen than susceptible ones.

The largest portion of the soluble nitrogen of pea plant is in the form of free amino acids. If the total free amino acids of pea plant juice is measured by the Van Slyke gasometric method, one finds that susceptible varieties contain a higher concentration of free amino acids than do resistant varieties. This result was also demonstrated by preliminary analyses with paper partition chromatography (3).

Finally, we have been able to analyse quantitatively each free amino acid in the plant juice of resistant and susceptible varieties, by using a new ultramicro quantitative method of paper chromatography developed at the University of Montreal (2). Preliminary results obtained in the last two summer seasons at the St-Jean Laboratory, show that the quantitative differences in nitrogen between two varieties, one resistant, the other susceptible, are largely due to differences in essential amino acids. In the case of arginine, threonine and valine, three amino acids known to be essential in insects and most other animals, large and usually consistent differences in concentration are observed between resistant and susceptible pea varieties, during most of the growing period of the plants. In susceptible varieties, the concentration in these three essential amino acids is from two to three times higher than in resistant varieties. Smaller but still significant differences are observed in other essential amino acids such as tryptophan, leucine and/or isoleucine, cystine and lysine. On the other hand, the amino acid alanine which, to our knowledge, has never been found essential for any insect studied so far, is present in about equal amounts in resistant and susceptible varieties. The same remark applies for other usually non essential amino acids such as glutamic acid, proline, the amide glutamine and a few others.

Preliminary results of the same kind have been obtained with different varieties of potatoes.

These differences are very interesting when interpreted as factors of resistance or susceptibility toward aphid infestation. The working hypothesis is as follows: Aphids feeding on resistant varieties will not obtain enough of each essential amino acid to sustain a *rapid* rate of growth, development and reproduction. In other words, on varieties poor in essential amino acids, aphid growth, development and reproduction will proceed at a much lower rate than on varieties rich in essential amino acids. This would cause the total aphid population on resistant varieties to be always or almost always smaller, (ratio of 1 to 8 or 1 to 10 aphids) than the aphid population on susceptible varieties. These differences in pea aphid population are significant enough to be of practical importance in the growing of canning pea for commercial purposes.

From these analytical results, it seems very probable that essential amino acids constitute an important factor of plant resistance to aphids.

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(9) Maltais, J. B. The nitrogen content in different varieties of peas as a factor affecting infestation by *Macrosiphum pisi* (Kltb.). *Can. Ent.* 83: 29-33. 1951.
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Some Additions and Corrections to the Species List of North American Agromyzidae (Diptera)[1]

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Further study, following submission for publication of the generic revision and species list (Frick, 1952), has resulted in changing the generic position of nine species, in making five synonymies, and in the addition of three subgenera and fifteen species to the list.

Malloch (1913, 1914) was reluctant to synonymize many North American species with European species due to the lack of positive identifications. Palaearctic species in the family Agromyzidae are now well defined as a result of the efforts of Hering, de Meijere, and Hendel (Hendel, 1931-1936). Therefore, the writer has not hesitated to synonymize North American species when there was an opportunity to study specimens, including leaf mines as well as adults, of the species in question.

The writer wishes to take this opportunity to thank Mr. C. W. Sabrosky for reading the manuscript and making several valuable suggestions and for the loan of specimens, including paratypes, of many species; to Dr. H. H. Ross for the permission to study Malloch's types at Urbana and for the use of the excellent facilities of his department; and to Dr. E. M. Hering, of Berlin, for the exchange of many species and for the loan from the Zoologisches Museum collection of certain critical species.

Genus *Agromyza* Fallén

Agromyza diversa Johnson

Agromyza diversa Johnson, 1922, Occ. Papers Bost. Soc. Nat. Hist., 5 : 26. This species was placed in the genus *Liriomyza* on the basis of the description (Frick, 1952). A study of a specimen collected of the University of Illinois, on July 15, 1945, shows that it belongs here and that the species is very similar to *A. ferruginosa* van der Wulp, 1871.

Agromyza reptans Fallén

Agromyza reptans Fallén, 1823, Dipt. Suec., 37 : 3; Melander, 1913, Jour. N.Y. Ent. Soc., 21 : 253, 254; Frick, 1952, Univ. Calif. Publ. Ent., 8 : 373.

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[1]Scientific paper No. 1113, Washington Agricultural Experiment Stations, Pullman.

Agromyza dubitata Malloch, 1913, Ann. Ent. Soc. Amer., 6 : 311. New synonymy.

A comparison of 3 paratypes of *A. dubitata* with a long series of *A. reptans* reared from *Urtica* sp. places Malloch's species as a synonym. This synonymy explains why *A. reptans* has not been reported from the eastern United States, although it has long been known from the Pacific Coast states. The known distribution now includes Massachusetts, Illinois, eastern Canada, and the three Pacific Coast states.

Genus *Melanagromyza* Hendel

Melanagromyza burgessi (Malloch), new combination

Agromyza burgessi Malloch, 1913, Ann. Ent. Soc. Amer., 6 : 323; Frick 1952, Univ. Calif. Publ. Ent., 8 : 378 (as a synonym of *M. lappae*).

A study of a paratype and two other specimens shows that this species is not a synonym of *M. lappae* (Hendel, 1931; Frick, 1952). The lunule is low, the orbital setulae are both upwardly and anteriorly directed, and the margin and fringe of the calypter are black. Reported from eastern and midwestern United States.

Genus *Phytobia* Lioy

Two changes in the key to subgenera (Frick, 1952) may be noted here. *Nemorimyza* Frey may be separated from *Phytobia* by the characters given under that subgenus. In the first part of couplet 7, the word "usually" should be added so that it reads: mesonotum with 3 + 1 dorsocentral setae; femora yellow, or if black, then with apices usually yellow.

Subgenus *Nemorimyza* Frey[1]

Nemorimyza Frey, 1946, Not. Ent., 26 : 42.

Type.—*Agromyza posticata* Meigen, 1830, monobasic.

A. posticata was placed in the subgenus *Dendromyza* (synonym of *Phytobia*) by Hendel (1931). It was removed by Kangas (1935), who restricted the *Dendromyza* species to those the larvae of which mine in cambium. Frick (1952), unaware of Frey's paper, placed *A. posticata* in the subgenus *Phytobia* and pointed out other diverse species maintained in the same subgenus.

Nemorimyza may be separated from *Phytobia* by the following characters which substantiate the erection of this subgenus: 3 + 0 dorsocentral setae; margin and fringe of calypter white; abdomen of males primarily yellow; and the larvae, which are leaf miners.

Subgenus *Phytobia* Lioy

Phytobia (Phytobia) indecora (Malloch), new combination

Agromyza indecora Malloch, 1918, Canad. Ent., 50 : 132; Frick, 1952, Univ. Calif. Pub. Ent., 8 : 375.

There are 38 specimens from White Heath, Illinois, in the Natural History Survey collection. This species belongs to the atypical group in the subgenus in which the costa ends at R_{4+5}, there is only 1 seta on the mid-tibia, and the antennal bases are separated by nearly the width of the first antennal segment. *P. indecora* is, therefore, closely related to *P. laticeps* (Hendel), 1931, and *P. lunulata* (Hendel), 1920.

Subgenus *Cephalomyza* Hendel

Phytobia (Cephalomyza) albidohalterata (Malloch), new combination

Agromyza albidohalterata Malloch, 1916, Psyche, 23 : 52; Frick, 1952, Univ. Calif. Publ. Ent., 8 : 372.

1L. nemoris (from nemus), a pasture, a woodland glade; plus myzon, sucker.

This is another annectant species within the genus. The species is placed in this subgenus because of an epistoma, genovertical plates markedly raised above the eye margins, only 1 upper fronto-orbital seta dorsally and outwardly directed, the lower upper fronto-orbital is separated and directed inward with the 3 lower fronto-orbital setae, frontal vitta, antennae, and most of the mesofacial plate yellow, and the legs black. Atypical *Cephalomyza* characters include: gena only one-third the eye height, mesofacial plate with antennal grooves brownish, and 2 minute setulae on the dorsal margin of the anepisternum.

Subgenus *Poëmyza* Hendel

Frey (1946) presents a key to the known Palaearctic species, several of which he described as new.

Phytobia (Poëmyza) lateralis (Macquart), new combination

Agromyza lateralis Macquart, 1835, Hist. Nat. Insect., Dipt., 2 : 609.

Dizygomyza (*Poëmyza*) *lateralis* (Macquart): Hendel, 1931, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 40.

Agromyza vittigera Zetterstedt, 1848, Dipt. Scand., 7 : 2760.

Agromyza variceps Zetterstedt, 1860, Dipt. Scand., 14 : 6453.

Agromyza laminata Brischke, 1881, Schrift. Naturf. Ges. Danzig, 5 : 53.

Agromyza coquilletti Malloch, 1913, Ann. Ent. Soc. Amer., 6 : 295.

Phytobia (*Poëmyza*) *coquilletti* (Malloch): Frick, 1952, Univ. Calif. Publ. Ent., 8 : 392. New synonymy.

Hering arranged a loan of specimens from the Zoologisches Museum to compare with specimens of *A. coquilletti*. The larvae are grass miners and have been reported mining the leaves of oats, barley, and wheat in the United States. Found throughout the United States and much of Canada.

Subgenus *Calycomyza* Hendel

Phytobia (Calycomyza) solidaginis (Kaltenbach), new combination

Agromyza solidaginis Kaltenbach, 1869, Verh. naturh. Ver. preuss. Rheinl. und Westphal., 26 : 196.

Dizygomyza (*Calycomyza*) *solidaginis* (Kaltenbach): Hendel, 1931, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 69.

Dizygomyza bellidis (Kaltenbach, 1858), Hendel p.p., 1920, Arch. Nat. Abt. A., 84 : 136.

In Europe the larvae of this species mine the leaves of *Solidago virgaurea* L. The writer has not reared the species but has a series swept from vegetation at Hope Valley, Alpine County, California.

Phytobia (Calycomyza) verbenae (Hering), new combination

Dizygomyza (*Calycomyza*) *verbenae* Hering, 1951, Not. Ent., 31 : 42.

Hering includes a key to Holarctic species by which this species may be separated from the other known species. It is closely related to *P. artemisiae* (Kaltenbach) as shown by the black margin and fringe of the calypter. The larvae form blotch mines in the leaves of cultivated varities of *Verbena hybrida*. The type specimens were reared by J. R. Eyer, at Las Cruces, New Mexico.

Subgenus *Trilobomyza* Hendel

Phytobia (Trilobomyza) calyptrata (Hendel), new combination

Agromyza nigrisquama Malloch, 1916, (*nec* Malloch, 1914) Psyche, 23 : 53.

Agromyza calyptrata Hendel, 1923, Konowia, 2 : 145; Frick, 1952, Univ.

Calif. Publ. Ent., 8 : 372.

A study of the type revealed that the species is typical for this subgenus. This is the first record of a species of *Trilobomyza* from North America.

Phytobia (Trilobomyza) pleuralis (Malloch), new combination

Agromyza pleuralis Malloch, 1914, Ent. News, 25 : 311; Frick, 1952, Univ. Calif. Publ. Ent., 8 : 375.

Agromyza clara (Melander), Frost, 1924, Cornell Mem., 78 : 41. New synonymy.

This is an example of another atypical species. It is placed here because it has more characters in common with *Trilobomyza* then with any other subgenus. Eight specimens, reared from larvae mining the leaves of *Catalpa bungei* by J. S. Houser at Wooster, Ohio, were indentical with Malloch's type, which was swept from *Catalpa* sp. Ohio, Illinois.

Subgenus *Praspedomyza* Hendel

Phytobia (Praspedomyza) morio (Brischke), new combination

Agromyza morio Brischke, 1881, Schrift. Naturf. Ges. Danzig., 5 : 26.

Dizygomyza (*Praspedomyza*) *morio* (Brischke): Hendel, 1931, IN Lindner: Die Flieg. Palaearkt. Reg., 59 : 80.

The writer has compared specimens of adults and leaf mines with those sent by Hering reared from *Galium aparine* L. in Europe. The California host plants are *Galium trifidum* L. and *A. aparine* from which adults were reared at Camino, El Dorado County, California.

Phytobia (Praspedomyza) subinfumata (Malloch), new combination

Agromyza subinfumata Malloch, 1915, Proc. U. S. N. M., 49 : 108; Frick, 1952, Univ. Calif. Publ. Ent., 8 : 375.

A study of the type places the species here. This species, together with *P. morio*, are the first records of species that are typical of the subgenus *Praspedomyza* from North America.

Subgenus *Dizygomyza* Hendel

Phytobia (Dizygomyza) luctuosa (Meigen)

Agromyza luctuosa Meigen, 1830, System. Beschr. bekann. eur. zweifl. Insekt., 6 : 170.

Agromyza laterella (Zetterstedt), Malloch p.p., 1913, Ann. Ent. Soc. Amer., 6 : 300.

Certain specimens, in the U. S. National Museum collection, identified as *Agromyza laterella* Zetterstedt, proved to be of this species. The larvae are known as leaf miners of *Carex* spp. and *Juncus* spp. in Europe.

Phytobia (Dizygomyza) morosa (Meigen), new combination

Agromyza morosa Meigen, 1830, System. Beschr. bekann. eur. zweifl. Insekt., 6 : 170.

Dizygomyza (*Dizygomyza*) *morosa* (Meigen): Hendel, 1931, IN Lindner Die Flieg. palaearkt. Reg., 59 : 90.

Agromyza atricornis Meigen, 1838, System. Beschr. bekann. eur. zweifl. Insekt., 7 : 399.

Agromyza laterella Zetterstedt, 1840, Ins. Lapp., 5 : 788; Malloch p.p., 1913, Ann. Ent. Soc. Amer., 6 : 300.

Dizygomyza laterella (Zetterstedt): Hering, 1926, Zeit. Morph. Oekol. Tiere, 5 : 481.

Agromyza riparia v. d. Wulp p.p., 1871, Tijdschr. Ent., 14 : 205.

Agromyza flaviventris Strobl, 1898, Mitt. Naturwiss. Ver. Steier., 34 : 271.

Phyllomyza fasciata Strobl, 1880, Obergymnasiums Benedikt., Programm, 14 : 38.

Specimens in the Illinois Natural History Survey collection, labelled *A. lateralis*, and a long series in the U. S. National Museum collection, labelled *A. laterella*, belong to this species. The larvae mine the leaves of *Carex* spp. in Europe. Widespread in Europe, North Africa, and North America.

Genus *Liriomyza* Mik

Liriomyza congesta (Becker)

Agrimyza trifolii (Burgess): 1880 (*nec* Kaltenbach, 1874), Ann. Rept. U.S. Dept. Agric., 1879 : 201 (as *Oscinis*). Secondary homonym. New synonymy.

Liriomyza trifolii (Burgess): Frick, 1952, Univ. Calif. Publ. Ent. 8 : 405. New synonymy.

Agromyza congesta Becker, 1903, Mitt. zool. Mus., 2 : 190.

Liriomyza congesta (Becker): Hendel, 1931, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 213.

Agromyza pusilla (Meigen), Malloch p.p., 1913, Ann. Ent. Soc. Amer., 6 : 278; Webster and Parks p.p., 1913, Jour. Agric. Res., 1 : 59.

Liriomyza pusio (Meigen), Hendel, 1920, Ach. Nat., Abt. A., 84 : 143.

Liriomyza leguminosarum de Meijere, 1924, Tijdschr. Ent., 67 : 141.

Mr. Sabrosky states (in correspondence) that the type of *A. trifolii* does not exist in the U. S. National Museum collection. As it seems probable that it was this common species that Burgess described, the synonymy is here made until the status of *A. trifolii* can be further clarified.

The writer has a long series of *L. congesta* reared from *Trifolium* spp., *Medicago sativa* L., *Melilotus* spp., and *Vicia* spp. This is the species with which Webster and Parks were primarily concerned. Found throughout Europe, central Asia and North America.

Liriomyza eupatorii (Kaltenbach)

Agromyza eupatorii Kaltenbach, 1874, Pflanzenfeinde, pg. 320 (reared from *Eupatorium*, *nec* from *Valeriana*, pg. 313).

Liriomyza eupatorii (Kaltenbach): Hendel, 1920, Arch. Nat., Abt. A., 84 : 143; de Meijere, 1925, Tijdschr. Ent., 68 : 283; Hendel, 1931, IN Lindner; Die Flieg. palaearkt. Reg., 59 : 217.

Kaltenbach's first description of this species (pg. 313) was of adults reared from larvae mining *Valeriana*, the second was of adults from *Eupatorium* (pg. 320). Hendel (1931) found two species were involved and, as the first reviser, chose to restrict the name *eupatorii* to the species mining *Eupatorium*. Hendel described the species mining *Valeriana* as a new species, *L. valerianae*. As this procedure certainly

avoids confusion between the specific names and the larval host plants, the writer is in full accord with Hendel's decision and ignores page preference in this case.

In Europe the larvae mine the leaves of *Eupatorium*, *Galeopsis*, *Lampsana*, and *Solidago* spp. The writer has reared the species from *Solidago gigantea* in the Yakima Valley, Washington, where it is very common.

Liriomyza verbenicola Hering

Liriomyza verbenicola Hering, 1951, Not. Ent., 31 : 43.

Hering compares this species to the closely related European *L. strigata* (Meigen), 1830. The larvae were reared from linear mines in the leaves of *Verbena* sp. in New Mexico by J. R. Eyer. Hering also has identified a mine from Salt Lake City, Utah, as belonging to this species.

Genus *Haplomyza* Hendel

Haplomyza minuta (Frost), new combination

Phytomyza minuta Frost p. p., 1924, Cornell Mem., 78 : 86.

A study of the type series reveals that the species belongs in the genus *Haplomyza* because the orbital setulae are dorsally directed, the costa continues to M_{1+2}, and M_{1+2} is as strong as R_{4+5}.

One cotype of the type series from Fargo, North Dakota, is distinct. This specimen is here designated the lectotype of *H. minuta* (Frost). The other three cotypes belong to *H. togata* (Melander) and are placed under that species. Ten specimens reared from *Chenopodium album* L. by the writer are the same as the lectotype and have been designated homotypes. This species may be distinguished from *H. togata* by the darkened third antennal segment and the narrow yellow color of the scutellum, which is so narrow that the distal pair of scutellar setae arise from the edge of the lateral black triangles.

Lectotype ♀: Fargo, North Dakota, June 13, 1918, U. S. N. M. Paratype No. 50029; deposited in the U. S. National Museum.

Homotypes: 1 ♂, 3 ♀ ♀, August 17, 1949; 1 ♂, 1 ♀, August 19, 1949, 1 ♂, September 21, 1949; 1 ♂, 1 ♀, June 28, 1950; 1 ♀, July 27, 1950; all reared from leaf mines on *Chenopodium album* L. by K. E. Frick at Prosser, Benton County, Washington.

Haplomyza togata (Melander)

Haplomyza togata (Melander), 1913, Jour. N. Y. Ent. Soc., 21 : 250; Frick, 1952, Univ. Calif. Publ. Ent., 8 : 410.

Phytomyza minuta Frost p.p., 1924, Cornell Mem., 78 : 86. New synonymy.

Three specimens of the cotype series, from Las Cruces, New Mexico, Marfa, Texas (labelled type but not published as such), and Bismark, North Dakota, proved to be identical to specimens reared from *Amaranthus retroflexus* L. and *A. hybridus* L. in California. Two other maier at Manhattan, Kansas, August 26, 1949. The distribution now in- specimens were reared from *Amaranthus retroflexus* L. by C. Steg- cludes Washington, California, New Mexico, Texas, Kansas, and North Dakota.

Genus *Phytagromyza* Hendel

Phytagromyza lonicerae (Robineau-Desvoidy)

Phytomyza lonicerae Robineau-Desvoidy, 1851, Rev. Mag. Zool., 3 : 396; Hendel, 1936, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 526.

Phytagromyza lonicerae (Robineau-Desvoidy): Hering, 1951, Not. Ent., 31 : 36.

Hendel did not recognize the species from the original description. Hering, however, resurrected the name for a species mining *Lonicera morrowii* Grey very early in the spring in Europe. The writer reared this species from *Symphoricarpos albus* (L.) and *Lonicera involucrata* Banks in March and early April at Berkeley, California. Hering compared the adults and mines with the neotype. There is only one generation a year in California.

Phytagromyza nitida (Malloch), new combination.

Agromyza nitida Malloch, 1913, Ann. Ent. Soc. Amer., 6 : 288; Frick, 1952, Univ. Calif. Publ. Ent., 8 : 373.

A study of the type shows that this species belongs here. The orbital setulae are sparse, short, and upwardly directed, prescutellar setae are absent, and cross vein m-m in less than its own length from cross vein r-m. The mediproboscis and labella are elongate and both together are subequal in length to the eye height. The only other known species having the mouthparts elongate is *P. hamata* Hendel, 1932, which is quite different in other respects and does not appear to be closely related.

Genus *Phytomyza* Fallén

Phytomyza agromyzina Meigen

Phytomyza agromyzina Meigen, 1830, System. Beschr. bekann, eur. zweifl. Insekt., 6 : 191; Hering, 1927, Tierw. Deutschl., 6 : 134; Hendel, 1934, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 336.

Hering has recently confirmed, after studying specimens sent to him, that the common European miner of *Cornus* spp. occurs in North America. The writer has reared adults from larvae in mines in the leaves of *Cornus californica* Mey and *C. stolonifera* Michx. in California and Washington.

Phytomyza crassiseta Zetterstedt

Phytomyza crassiseta Zetterstedt, 1860, Dipt. Scand., 14 : 6469; Hendel, 1935, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 387.

The larvae of this species mine the leaves of *Veronica* spp. in Europe and the Canary Islands. The writer has reared adults from larvae mining the leaves of *Veronica peregrina* L. var. *xalapensis* (H.B.K.) at Prosser, Washington.

Phytomyza periclymeni de Meijere

Phytomyza periclymeni de Meijere, 1924, Tijdschr. Ent., 67 : 145; de Meijere 1926, Tijdschr. Ent., 69 : 218; Hering, 1927. Tierw. Deutschl., 6 : 148: Hendel, 1935, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 452.

Phytomyza nigritella (Zetterstedt), Melander, 1913, Jour. N. Y. Ent. Soc., 21 : 270; Frost p.p., 1924, Cornell Mem., 78 : 81.

Phytomyza obscurella (Fallén), Hardy, 1849, Ann. Mag. Nat. Hist., 4(24): 390.

Preliminary studies by Hering placed *P. nigritella* of Melander close to *P. periclymeni* (Frick, 1952). Both Hering and the writer now consider the species as a synonym. In Europe the larvae mine the leaves of *Lonicera* spp. and *Symphoricarpos* spp. and Hering (1927) gives a figure of the type of mine.

The writer found the species to be common at Berkeley, California, and in the Yakima Valley, Washington. Specimens have been reared from larvae in mined leaves of *Symphoricarpos albus* (L.) and a cultivated *Lonicera* sp.

Phytomyza rufipes Meigen

Phytomyza rufipes Meigen, 1830, System. Beschr. bekann. eur. zweifl. Insekt., 6 : 192; Hendel, 1935, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 471.

Phytomyza sulphuripes Meigen, 1830, System. Beschr. bekann. eur. zweifl. Insekt., 6 : 193.

Phytomyza ruficornis Zetterstedt, 1848, Dipt. Scand., 7 : 2825.

Phytomyza zetterstedti var. *genis latissimis* Strobl. 1893. Wien. Ent. Ztg., 12 : 136.

Phytomyza bistrigata Strobl, 1906, Real Soc. Span. Hist. Nat., 3(5): 384.

Phytomyza flavicornis (Fallén), Melander, 1913, Jour. N. Y. Ent. Soc., 21 : 270.

Hendel (1935) pointed out that Melander's specimen of *P. flavicornis*, obtained from Strobl, is a misidentification. Melander reports the species from Ohio, Illinois, and Alaska. The writer has studied 2 from Germany reared from *Brassica napus* by Hering and 3 from Plymouth, Devon, England, July 5, 1926, collected by C. L. Fox. These were compared with 7 specimens in the Oregon State College collection. Five are from Vernonia, Oregon, April 25, 1938, and 2 from three miles east of the Ochoco Ranger Station, May 3, 1939, collected by K. Gray and J. Shuh, by sweeping.

The larvae mine the leaves of species of *Armoracia, Diplotaxis*, and *Brassica*, especially the latter. The species is very widespread in Europe, the Near East, and north Africa.

Phytomyza spondylii Robineau-Desvoidy

Phytomyza spondylii Robineau-Desvoidy, 1851, Rev. Mag. Zool., 3 : 400; Hering, 1927, Tierw. Deutschl., 6 : 122; Hendel, 1935, IN Lindner: Die Flieg. palaearkt. Reg., 59 : 483.

Phytomyza albiceps (Meigen), Hardy, 1849, Ann. Mag. Nat. Hist., 4(24): 392.

Phytomyza nigra (Meigen), Goureau, 1851, Ann. Soc. Ent. France, (2)9 : 147.

Phytomyza heraclei Kaltenbach, 1862, Verh. naturh. Ver. preuss. Rheinl. und Westphal., 19 : 36.

Phytomyza fallaciosa Brischke p.p., 1881, Schrift. Naturf. Ges. Danzig, 5 : 23.

Hering confirmed that this species, the heracleum miner, occurs in North America. The writer has reared adults from larvae in mined leaves of *Heracleum lanatum* Michx. in various locations in California.

Supplement to the Reference List of New World Species

(Species names in italic type are either homonyms or synonyms)

Previous Generic Position	Present Generic Position
Agromyza albidohalterata Malloch, 1916	Phytobia (Cephalomyza) albidohalterata (Malloch), 1916
Agromyza burgessi Malloch, 1913	Melanagromyza burgessi (Malloch), 1913
Agromyza calyptrata Hendel, 1923	Phytobia (Trilobomyza) calyptrata (Hendel), 1923
Agromyza diversa Johnson, 1922	Agromyza diversa Johnson, 1922
Agromyza dubitata Malloch, 1913	Agromyza reptans Fallén, 1823
Agromyza indecora Malloch, 1918	Phytobia (Phytobia) indecora (Malloch), 1918
Agromyza laterella Zetterstedt, 1840	Phytobia (Dizygomyza) morosa (Meigen), 1830
Agromyza nitida Malloch, 1913	Phytagromyza nitida (Malloch), 1913
Agromyza pleuralis Malloch, 1914	Phytobia (Trilobomyza) pleuralis (Malloch), 1914
Agromyza subinfumata Malloch, 1915	Phytobia (Praspedomyza) subinfumata (Malloch), 1915
Agromyza trifolii (Burgess), 1880 (*nec* Kaltenbach, 1874)	Liriomyza congesta (Becker), 1903
Dizygomyza (Calycomyza) verbenae Hering, 1951	Phytobia (Calycomyza) verbenae (Hering), 1951
Dizygomyza (Calycomyza) solidaginis (Kaltenbach), 1869	Phytobia (Calycomyza) solidaginis (Kaltenbach), 1869
Dizygomyza (Dizygomyza) morosa (Meigen), 1830	Phytobia (Dizygomyza) morosa (Meigen), 1830
Dizygomyza (Poëmyza) lateralis (Macquart), 1835	Phytobia (Poëmyza) lateralis (Macquart), 1835
Dizygomyza (Praspedomyza) morio (Brischke), 1881	Phytobia (Praspedomyza) morio (Brischke), 1881
Liriomyza congesta (Becker), 1903	Liriomyza congesta (Becker), 1903
Liriomyza eupatorii (Kaltenbach), 1874	Liriomyza eupatorii (Kaltenbach), 1874
Liriomyza trifolii (Burgess), 1880	Liriomyza congesta (Becker), 1903
Liriomyza verbenicola Hering, 1951	Liriomyza verbenicola Hering, 1951
Phytagromyza lonicerae (Robineau-Desvoidy), 1851	Phytagromyza lonicerae (Robineau-Desvoidy), 1851
Phytobia (Phytobia) posticata (Meigen), 1830	Phytobia (Nemorimyza) posticata (Meigen), 1830
Phytobia (Poëmyza) coquilletti (Malloch), 1913	Phytobia (Poëmyza) lateralis (Macquart), 1835
Phytomyza agromyzina Meigen, 1830	Phytomyza agromyzina Meigen, 1830
Phytomyza crassiseta Zetterstedt, 1860	Phytomyza crassiseta Zetterstedt, 1860
Phytomyza minuta Frost p.p., 1924	Haplomyza minuta (Frost), 1924
Phytomyza minuta Frost p.p., 1924	Haplomyza togata (Melander), 1913
Phytomyza periclymeni de Meijere, 1924	Phytomyza periclymeni de Meijere, 1924
Phytomyza rufipes Meigen, 1830	Phytomyza rufipes Meigen, 1830
Phytomyza spondylii Robineau-Desvoidy 1851	Phytomyza spondylii Robineau-Desvoidy, 1851

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Rapid Method for Mounting Nematodes in Glycerine[1]

By A. D. Baker[2]

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The prevailing method of preparing glycerine mounts of nematodes consists essentially of transferring the specimens from the fixative to 1.5-2.0 per cent glycerine in water and then allowing the water to evaporate very slowly until the nematodes are in pure glycerine. By this method evaporation is completed in not less than four weeks as any attempt to hurry this process will distort the specimens. A desiccator is used to complete the removal of the water from the glycerine.

By the following method nematodes may be transferred from fixative to glycerine in about one hour:—

1. Relax and kill specimens in usual manner (water and gentle heat).

2. Transfer to 5 per cent formol and leave in fixative at least overnight. (Other formol fixatives may be used, such as formol-acetic and Ditlevsen's.)

3. Transfer specimens from fixative to lactophenol in hollow-cavity slide. Warm gently to a temperature of about 65°C. (Stain may be included with the lactophenol, as described by Franklin and Goodey in 1949.)

4. Transfer specimens to a heated quantity of mixture A. (See formulae.) Heat to a temperature not exceeding 50°C. Allow specimens to remain in this

Formulae

	Mixture				
	A	B	C	D	E
Glycerine	50	60	70	80	90
Distilled water	35	25	15	5	2.5
Lactic acid	5	5	5	5	2.5
Phenol	5	5	5	5	2.5
Formol	5	5	5	5	2.5

With lactophenol the proportions would be as follows:—

	A	B	C	D	E
Lactophenol	25	25	25	25	12.5
Glycerine	40	50	60	70	85.0
Water	30	20	10	0	0
Formol	5	5	5	5	2.5

1Contribution No. 3065, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada.

2In charge of Section.

mixture for 10 minutes. (Fresh quantities of all these mixtures should be used each time as repeated heating will alter their composition through evaporation.)

5. Transfer specimens to mixture B. Same procedure as No. 4.

6, 7, and 8. Same procedure as No. 4, using mixtures C, D, and E.

9. Transfer specimens to pure glycerine. (Or place open container in desiccator while specimens are still in mixture E.)

10. Place open container in desiccator.

11. Mount in anhydrous glycerine.

Good mounts may be obtained by omitting step No. 10, but the keeping quality of such specimens is not yet clear.

A somewhat slower method is to follow the above procedure until the specimens are in mixture A (steps 1-4). Specimens may then be placed in small Syracuse watch glasses filled to the top with mixture A and these containers then placed in a large Petri dish which is covered and partly sealed. Slow evaporation can then be accomplished in 8-10 days, when transfers may be made to pure glycerine. As with the standard method the evaporation rate has to be controlled carefully.

Canada balsam may be used for ringing glycerine mounts, either alone or after a ringing with Zut. Cover glasses are then less liable to side-slip when removing immersion oil but are somewhat more difficult to remove if remounting of the specimen is desired.

A Recently Introduced Species of European Grasshopper

By F. A. URQUHART[1] AND J. R. BEAUDRY[2]

It is important to record in the literature at this time the occurrence of *Roeseliana roeselii* (Hag.)[3] in the province of Quebec. The specimens were collected by J. R. Beaudry at Ville Saint-Laurent (12-VII-52, 2 ♂ ♂; 13-VII-52, 3 ♂ ♂) and at Montreal (16-VII-52, 1 ♂; 19-VII-52, 1 ♂).

This particular species is of common occurrence in Europe. Its distribution is given by F. E. Zeuner[4] as "Spain, France, England, central, east, and south-east Europe, southern Ural Mts., Tomsk, and Siberia."

It was most likely introduced into Quebec by aircraft because the specimens were taken near the airports of Montreal.

In view of the wide distribution of this species in Europe, where it occurs in considerable numbers, it is believed that it will become well established in Quebec and will eventually extend its range over much of the eastern United States and Canada.

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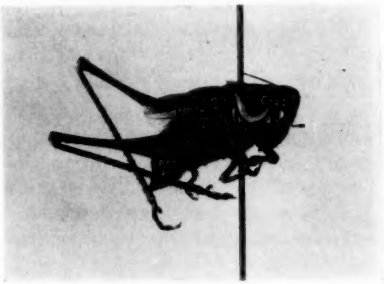
3*Platycleis roeselii* (Hag.); *Metrioptera roeselii* Hag.

4The classification of the Decticinae hitherto included in *Platycleis* Fieb. or *Metrioptera* Wesm. (Orthoptera, Saltatoria); Trans. Roy. Ent. Soc., London, Vol. 91, Pt. 1, Pp. 1-50, '41.

5Additions à la faune orthoprérologique de la province de Québec ou du Canada: Ann. de l'Acfas, Vol. 18, Pp. 100-102, '52.



The specimens agree in every detail with those collected in Germany by E. M. Walker (specimens contained in the collection of the Royal Ontario Museum of Zoology and Palaeontology).

We also wish to report the occurrence of *Psinidia fenestralis* (Serville) in Berthier, Quebec. One male specimen was collected by J. R. Beaudry and A. Robert on August 4, 1951. The occurrence of this particular species in Quebec was previously recorded by J. R. Beaudry[5].

One specimen of *R. roeselii* will be retained in the collection of the Royal Ontario Museum of Zoology and Palaeontology, and six specimens will be retained in the collection of the Institut de Biologie of the Université de Montréal.

The specimen of *P. fenestralis* is in the collection of the Institut de Biologie of the Université de Montréal.

BROTHER JOSEPH OUELLET, C.S.V.
1869-1952

The death of Brother Joseph Ouellet, C.S.V. occurred in Montreal on January 9th, 1952 in his eighty-third year. The passing of this kindly and generous-hearted man and life-long student of insects should not be allowed to go unrecorded in the pages of this journal which was born a scant few months earlier than he. For the following brief details of his career I have relied partly on the excellent Memoir by Brother Adrien Robert, C.S.V., published in the March 1952 number of "Sciences et Aventures".

Joseph Ouellet was born at Levis in 1869. He completed his formal education in 1884, and was admitted to the Brotherhood of "Clercs de Saint-Viateur", commencing at once the teaching which was to be his life-long profession. He early developed an absorbing interest in natural history and spent his vacations roaming the countryside, collecting, at first, plants and insects, but later concentrating his energies on Entomology.

He was a contemporary collector, at Levis, with the celebrated Dr. Fyles, but, once launched in his career, his visits to his home were probably of short duration, and it is not recorded that they ever met.

As time went on, his knowledge of the Quebec insect fauna became unrivalled and, on the formation of the Entomology Department of the Université de Montréal in 1931, he was obliged—much against his will, for he shunned the limelight—to assume the chair of Systematic Entomology. To this position he

brought the lustre of a perceptive and well-trained mind and the energy of a man of half his years. He served the University actively for 10 years and, after his retirement, continued to enrich its collections with the fruits of his summer excursions, for he remained an indefatigable collector to the last year of his life.

Brother Ouellet was exceptionally meticulous in his curatorial work. His specimens were beautifully mounted and, for this reason, leading specialists everywhere were glad to identify material for him and to exchange specimens. To improve the appearance or utility of his material no task was too tedious. Having decided that his labels, printed in 10-point type, were too large, he proceeded to relabel the entire collection, then about 30,000 specimens, using 6-point type. Future students will benefit from his habit of placing an identification label with the name of the determiner on each specimen. He was not a prolific writer and in a period of forty years I can find only eleven papers, all published in "Le Naturaliste Canadien". His later writings show a preference for the order Diptera.

In 1941 he discovered and described the rare and beautiful larvaevorid fly *Archytas currani* Ouell., but most unluckily, Reinhard had described the same species as *Exopalpus pompalis* Rnh. only a few months earlier. His collection contains other unique Canadian records too numerous to mention.

Brother Ouellet was of slight stature and scholarly appearance. His outstanding personal characteristics were his gentleness of manner, evident humility and perfect courtesy.

I shall not forget our first meeting, when I visited him to ask for the loan of some material for a thesis. Having conducted me to his room and showed me the cabinet that housed his collection, he explained that he would have to return to his classroom duties and, spreading out his arms in a large French gesture, he asked me, if I would please help myself to whatever I needed. He then excused himself and left me.

He was held in great affection and respect by both pupils and colleagues and, in recognition of his services, the Conseil de l'Instruction Publique, in 1930, awarded him its "Ordre du mérite scholaire". With his passing Canada has lost an outstanding naturalist. Fortunately his collection will be well cared for. It will be housed in the Museum of the Institution des Sourds-Muets in Montreal, where he did so much of his teaching. Brother Adrien Robert, C.S.V. has been appointed its curator and enquiries should be addressed to him at 480, Querbes, Outremont, Montreal 8, Que.

G. E. SHEWELL.

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